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UNIVERSITY OF CALIFORNIA,
IRVINE

Climate Driven Range Shifts Impact Communities Through Altered Species Interactions

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

Piper D. Wallingford

Dissertation Committee:
Assoc. Professor Cascade Sorte, Chair
Professor Matthew Bracken
Professor Kailen Mooney

2020

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Publications

- Wallingford, PD**, TL Morelli, JM Allen, EM Beaury, DM Blumenthal, BA Bradley, J S. Dukes, R Early, EJ Fusco, DE Goldberg, I Ibáñez, BB Laginhas, M Vilà, and CJB Sorte. 2020. Assessing impacts of climate-driven range shifts through the lens of invasion biology. *Nature Climate Change* 10:398–405.
- Wallingford, PD** and CJB Sorte. 2019. Community regulation models as a framework for direct and indirect effects of climate change on species distributions. *Ecosphere* 10(7): e02790.
- Sorte, CJB, G Bernatchez, LLM Pandori, NJ Silbiger, AS Smith and **PD Wallingford**. 2019. Thermal tolerance limits as indicators of current and future intertidal zonation patterns in a diverse mussel guild. *Marine Biology* 166:6.
- Wallingford, PD**, LLM Pandori, SA Bedgood, MES Bracken, LA Elsberry, AK Henry, SA Mahanes, and CJB Sorte. 2018. A guide to the relationships between marine spatial patterns and ecological processes. *Frontiers of Biogeography* 10(3-4): e39410.

Forthcoming Publications

- Wallingford, PD** and CJB Sorte. *Mexacanthina* on the move: Range shifts of the dark unicorn whelk. *Manuscript in prep (available on request)*.

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- Comparing microbiomes of endemic and range-expanding whelks in Southern California. In collaboration with L. Khadempour at Cal State, Northridge.

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2010	Inducted to Phi Beta Kappa International Honour Society
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2006-2010	NYU College of Arts and Sciences Scholarship (\$100,000)
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Research Experience

- | | |
|------------|--|
| 2018-2020 | Graduate Researcher at <i>University of California, Irvine</i> – Led observational and manipulative experiments to assess the effects of climate change on predator-prey interactions in intertidal communities. |
| 2018-2019 | Graduate Researcher at <i>Northeast Regional Invasive Species and Climate Change (RISCC) Management Network</i> – Conducted literature reviews on invasive species publications and developed research reviews for distribution to management and conservation stakeholders. |
| 2013- 2015 | Senior Environmental Scientist at <i>Advanced Cleanup Technologies</i> – Conducted environmental assessments and historical reviews of properties to assess levels of environmental contaminants. |
| 2012 | Science and Protected Species Intern at <i>Oceana</i> – Co-authored an investigative report documenting compliance and effectiveness of turtle excluder devices in the Gulf of Mexico. Assisted with literature reviews, data analysis, and policy drafting. |
| 2011 | Researcher at <i>University of Miami Shark Research and Conservation Program</i> – Assessed changes in fish anti-predator behaviors along risk and refuge gradients in mangrove and reef ecosystems. Conducted shark tagging surveys and collected biological samples. |

- 2008- 2010 Project Safe Flight Program Coordinator at *New York City Audubon Society* – Collected and analyzed data to determine which city buildings saw the highest numbers of bird strikes in Manhattan. Participated in population counts and banding of great egret chicks, analyzed long-term population data of wading bird colonies in New York Harbor.
- 2008 Research Intern at *New York City Audubon Society* –Coordinated data collection of migrating bird populations throughout New York City.

Teaching Experience

University of California, Irvine

Co-Instructor

Cli Fi: The Science of Climate Fiction (2017-2018)

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Ecology 179L: Freshwater Field Ecology Lab (2016-2019)

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Biology 94: Organisms to Ecosystems (2016, 2018)

Biology 120: Human Biology (2019)

Ecology 106: Ecology and Evolution (2017-2020)

Ecology 179L: Freshwater Field Ecology Lab (2016-2019)

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Mentoring

- 2018- 2019 Undergraduate researcher Deida Lopez – awarded Undergraduate Research Opportunities Program grant for individual research project (\$400). Presented at UCI Undergraduate Research Symposium.
- 2017- 2018 Undergraduate researcher Haley Heesch; Undergraduate researcher Eduardo Cruz – co-awarded Undergraduate Research Opportunities Program grant with R Singh for joint research project(\$800). Co-presented at UCI Undergraduate Research Symposium.
- 2016- 2018 Undergraduate researcher Ritika Singh – awarded Undergraduate Research Opportunities Program grant for individual research (\$400), co-awarded awarded Undergraduate Research Opportunities Program grant with E. Cruz, (\$800) Summer Undergraduate Research Program fellowship (\$1,000) and presented

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2015- 2016 Undergraduate researcher Savannah Todd.

2011 High school students Leo Alvarez and Vilma Sooknanin.

Public Outreach and Education

2018 Invited lecturer at Dana Point Science Night at the Dana Point Community Center. Dana Point, CA.

2018 Invited lecturer at Orange County Marine Protected Area Council Continuing Education Day at the Ocean Institute. Dana Point, CA.

2018 Research featured in Orange County Register (cover article). 23 February. "A Hunt for the Invasive Dark Unicorn Snail Shows UCI Students How Climate Change Is Altering Crystal Cove Tide Pools." Anaheim, CA

2017-2020 Led middle- and high-school girls in intertidal survey at Girls in Ocean Sciences Conference at the Ocean Institute. Dana Point, CA.

2017 Presenter at Annual Children's Water Festival. Irvine, CA.

2016-2017 Co-ran The Biology Bus, promoting conservation and women in science through social and traditional media. <https://www.thebiologybus.com/>

2016-2017 Collaborated with choreographer Koryn Ann Wicks to develop *Embodied Ecology*, presenting complex ecological data in an interactive environment that engages audience members. Presented in Irvine, CA; San Marco, TX; and Rome, Italy. <https://vimeo.com/204997804>

2015-2016 Environmental Educator at Sunday Open Houses at the Back Bay Science Center. Newport Beach, CA.

2013- 2015 Volunteer Dive Team Instructor at the New York Aquarium. Provided continuing education on conservation and marine biology to guests and other team members. Brooklyn, NY.

2011 Developed and ran conservation lectures and organized research trips for high school students through the University of Miami Shark Research and Conservation Program. Miami, FL.

2008-2010 Collaborated with middle and high school teachers to promote conservation and interest in STEM through guest lectures and development of in-class materials. New York, NY.

Professional Development

2019 Seminar in Ecology and Evolutionary Biology Education. Seminar on developing outreach programs for the general public.

2018 Seminar in Ecology and Evolutionary Biology Education. Seminar on pedagogy, developing and implementing active learning, and increasing equity in STEM fields.

- 2018 Northeast Regional Invasive Species & Climate Change (RISCC) Management Symposium. Interdisciplinary meeting between natural resource managers and scientists to discuss how climate change might affect invasion risk.
- 2018 Phenology Information & Tools for Invasive Species Management Meeting. Collaboration between scientists and research managers to develop tools for using phenological information in invasive species management.
- 2017 Enhancing Linkages between Mathematics and Ecology (ELME) Summer Program at Kellogg Biological Research Station, Michigan State University.
- Maximum Likelihood Analysis in Ecology (Dr. Colin Kremer, UCLA)
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 - Stochastic Modelling (Dr. Kevin Gross, North Carolina State University)
- 2016 Seminar in Bayesian Statistics. Semester-long seminar on theory and application of Bayesian statistics (Dr. Megan Donahue, University of Hawai'i Mānoa).

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ABSTRACT OF THE DISSERTATION

Climate driven range shifts impact communities through altered species interactions

by

Piper D. Wallingford

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2020

Associate Professor Cascade J.B. Sorte, Chair

Climate change is likely the greatest threat to global biodiversity and ecosystem functioning, and it is becoming increasingly apparent that understanding the effects of climate change requires going beyond single species or limited spatial scales. Climate change will impact species and communities through both direct and indirect effects, as mediated by species interactions, and incorporating these indirect effects can increase the ability to track shifting species distributions. In Chapter 1, I used a space-for-time approach to test if incorporating indirect effects increases predictive ability through surveys of vertical distributions of predators (sea stars) and prey species (mussels) spanning a thermal gradient along the West Coast. I found that prey distributions were directly influenced by temperature, but there was also a significant indirect effect of temperature, as mediated by predator distributions. Under future climate change, mussel ranges may undergo vertical shifts towards subtidal habitats, allowing for localized persistence of mussels and their associated species. However, both local and broad scale range-shifts can displace other species or alter community and ecosystem processes. In Chapter 2, I explored how risk assessments developed for invasive species could provide a useful tool for assessing potential impacts of range-shifting species. Despite inherent differences

between introduced and range-shifting species, I highlight the ways in which impacts can occur via analogous mechanisms, and the magnitude of impacts can be similar. Invasion ecology can be adapted to provide a framework for understanding the impacts of range-shifting species. An example of altered species interactions and communities can be observed locally in southern California intertidal communities, where the whelk *Mexacanthina lugubris* is undergoing a northward range shift. In my final chapter, I assessed the impacts of *Mexacanthina* on local species, through long-term field surveys, coupled with manipulative experiments to assess current and future impacts on competitors. *Mexacanthina* is now well established and utilizes analogous resources and habitats as native whelk species. *Mexacanthina* can also survive at warmer temperatures than native whelks, suggesting that range-shifters may have a competitive advantage in a warming climate. The persistence of some species at the expense of others underscores the complexities of conservation in the era of climate change. My thesis research explores this dichotomy by examining how species interactions can indirectly alter distributions (Ch. 1), which traits are indicative of problematic range-shifters (Ch. 2), and how a range-shifting species is altering southern California communities (Ch. 3).

INTRODUCTION

As Earth's climate changes, species persistence will depend on the ability of populations to respond to climate changes, either *in situ* through acclimation and adaptation, or by dispersing to less stressful environments (Williams et al. 2008, Dawson et al. 2011, Bellard et al. 2012).

Although species' responses occur on the individual and population levels, they are likely to also alter community dynamics due to altered species interactions. Species and population responses to climate change may occur at different scales and rates, and shifts in species ranges could alter existing communities by introducing novel species interactions. Furthermore, given that the extent of range shifts has only recently been acknowledged (Chen et al. 2011, Lenoir and Svenning 2015), the impacts of range shifts on existing communities is not well understood. My dissertation research focuses on the complex ways that climate change affects ecological communities through feedbacks between species distributions and biological interactions.

Climate-driven range shifts have been reported across taxa and ecosystems, leading to altered species' abundances and distributions (Parmesan 2006, Chen et al. 2011). Species distributions are changing more rapidly than they have in the past (Lawing and Polly 2011), with terrestrial species shifting away from the equator at a rate of 17 km per decade (Chen et al. 2011). and marine taxa at a rate of 72 km per decade (Sorte et al. 2010). Range shifts are also occurring along depth and elevation gradients, as changes in distributions, even at small spatial scales, can mitigate the effects of climate change. Given that 100 km toward the poles is roughly equivalent to a temperature decrease of 1°C (Hughes 2000), a downward shift of 1 m in intertidal elevation could similarly mitigate thermal stress for coastal species (Denny et al. 2009). Projecting how species are likely to respond to climate change, and in which direction, can therefore provide important information regarding potential extinctions and loss of biodiversity.

Predictions of future distributions are often based on species' tolerances to environmental conditions, namely temperature; however, such models are often over-simplified as they focus only on a single variable of the multitude that interact to set distributions. Climate envelope models, for example, use the climate of a species' current geographic distribution and extrapolate these distributions to projected conditions (Hijmans and Graham 2006, Thomas 2010). Although useful, such models are often inaccurate or incomplete due to over-extrapolation, large variability at the applied spatial scales, or the exclusion of mechanistic drivers (Moritz and Agudo 2013). For example, when climate envelope models were applied to 100 species of European birds, modeled climate-distribution associations did not fit significantly better than chance associations for more than more than 60% of the species (Beale et al. 2008). Another significant concern with only using species tolerances to generate range projections is that these models ignore the effects of biological interactions on species distributions (Araújo and Luoto 2007, Morales-Castilla et al. 2015), interactions which can have significant implications for community regulating mechanisms.

Species interactions, both positive and negative, play an important role in structuring ecological communities, and understanding the mechanisms and magnitude of their importance has been a driving question throughout modern ecological study (e.g. Hutchinson 1959, Hairston et al. 1960). For example, competition can lead to localized niche partitioning (Connell 1961, Tilman 1982) and drive speciation across both spatial and temporal scales (Pigot and Tobias 2013). Predation similarly influences the realized niche, limiting prey distributions through both mortality and risk-induced responses (Paine 1966, Werner and Peacor 2003). Facilitation, on the other hand, can expand a species' realized niche beyond its fundamental niche due to amelioration of abiotic stress (Bruno et al. 2003). Importantly, species interactions are often

context dependent and can shift with changing environmental conditions (Chamberlain et al. 2014). Considering species interactions can lead to better predictions of species distributions, and for predicting future distributions, the indirect effects of climate change as mediated through species interactions must also be taken into account.

As species undergo range shifts in response to climate change, they have the potential to alter species interactions and disrupt community dynamics in the areas where they establish. Previous studies have examined the magnitude of climate-induced range shifts and their effects on the individual and population scale, but few studies have examined the direct and indirect effects at the community level (Sorte et al. 2010). This is especially surprising as tools to assess the risks and benefits of a novel species already exist in the invasive species literature. While there are inherent differences between introduced and range-shifting species, namely a shared evolutionary history (Fridley and Sax 2014), impacts can occur via analogous mechanisms, and the magnitude of impacts can be similar (Sorte et al. 2010, Nackley et al. 2017, Bonebrake et al. 2018). Impacts for both introduced and range-shifting species are likely to be greatest 1) if species display wide dispersal, fast growth, high pathogen load, and the ability to modify the physical environment and 2) when the recipient community has a history of disturbance, naïve prey, and a lack of native competitors or predators (Catford et al. 2009).

Climate change is already altering communities and ecosystems both directly and indirectly, resulting in profound changes to biodiversity and ecosystem functioning on a global scale (Parmesan and Yohe 2003). Facilitating range shifts is therefore often recognized as a key climate change adaptation strategy with species persisting as they follow their climatic niches. While understanding species' tolerance limits can provide an initial framework for predicting climate change impacts on species' ranges, these models are likely to be incomplete if they fail

to account for biological interactions. Biotic interactions could facilitate or impede range shifts of other stressed species but moving into new communities will undoubtedly lead to changes to existing community dynamics. In some cases, range-shifting species will even displace other species or permanently alter community and ecosystem processes, which introduces significant management conundrums. Responding to the dilemma of some species persisting at the expense of others will likely be a continuing challenge in predicting and responding to climate change impacts. My dissertation research described here addresses the ways in which species interactions can indirectly alter distributions, potential impacts of range-shifting species, and how to assess these impacts by adapting invasive species ecology.

Literature Cited

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- Bonebrake, T. C., C. J. Brown, J. D. Bell, J. L. Blanchard, A. Chauvenet, C. Champion, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, A. I. Dell, J. M. Donelson, B. Evengård, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, M. A. Jarzyna, E. Lee, J. Lenoir, H. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, E. McDonald-Madden, N. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, H. Possingham, P. Pulsifer, M. Reynolds, B. R. Scheffers, C. J. B. Sorte, J. M. Strugnell, M.-N. Tuanmu, S. Twiname, A. Vergés, C. Villanueva, E. Wapstra, T. Wernberg, and G. T. Pecl. 2018. Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews* 93:284–305.
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- interactions? *Ecology Letters* 17:881–890.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
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CHAPTER 1

Community regulation models as a framework for direct and indirect effects of climate change
on species distributions

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Abstract

Existing projections of climate change impacts focus primarily on direct abiotic impacts on individuals and populations. However, these models often ignore species interactions, which are vital for determining community composition and structure. To evaluate both direct and indirect effects of climate change on species distributions, we applied the Menge–Sutherland model, which describes the relative role of predation and environmental stress in regulating community structure. Using a space-for-time approach, we tested the predictions that (1) predators are more strongly impacted by increasing environmental stress than prey (as described in the Menge–Sutherland model) and (2) incorporating indirect (predator) effects increases our ability to predict impacts of increased temperature on prey distributions. We surveyed vertical distributions of predators (sea stars) and a foundational prey species (mussels) at 20 intertidal sites spanning a thermal gradient along the West Coast of the United States. Using generalized linear models and structural equation models, we found that as temperature increased, the upper limits of foundational prey species decreased (a direct effect), while prey lower limits also shifted downward, due to an indirect effect of temperature on predator distributions. Under future climate change, mussel ranges may undergo vertical shifts toward subtidal habitats, allowing for localized persistence of mussels and associated species. Our model comparisons indicate that this framework—incorporating both direct and indirect environmental stress effects within a classic community regulation model—can improve prediction of responses to warming. Community regulation models could be expanded to inform management and conservation efforts during unprecedented climate and ecological change.

Introduction

Climate change is one of the greatest threats to global biodiversity and ecosystem functioning (Sala et al. 2000), and it is becoming increasingly apparent that predicting and mitigating the effects of ongoing and accelerating climate change require going beyond studies examining single species or spatial scales to understand the role of community-level interactions. Environmental stress affects organisms both directly, through altered physiology, as well as indirectly, through changes to species interactions (Fleeger et al. 2003, Adams 2005). While understanding species' tolerance limits and modeling these as a function of predicted environmental changes can provide an initial framework, it is also clear that models may be incomplete if biological interactions are not incorporated (Davis et al. 1998, Nagelkerken and Munday 2016). For example, in predicting responses of salt marsh plants to drought, models incorporating only physiological tolerance limits largely failed to simulate observed effects because plants experiencing sub-lethal stress were more vulnerable to mortality from herbivores (He et al. 2017). Here, we use an existing framework of consumer stress models (Hairston et al. 1960, Menge and Sutherland 1987), which incorporate both direct and indirect effects of environmental conditions, as a framework for ecological forecasting.

Direct effects of climate change

To date, the great majority of studies evaluating responses to climate change have focused on the direct effects of environmental conditions on individual physiology and population demographic rates (Davis et al. 1998, Keith et al. 2008). Physiological responses to changing environmental conditions include altered molecular (Hofmann 2005, Pörtner and Farrell 2008, Ahuja et al. 2010) metabolic rates (Sanford 1999, 2002, Dahlhoff 2004), growth

rates (Bale et al. 2002, Hoegh-Guldberg et al. 2007, Doney et al. 2009), behavior (Menzel et al. 2001), and, ultimately, mortality (Hughes et al. 2003, McKechnie and Wolf 2010, Carnicer et al. 2011). Such direct effects can also scale up to alter population dynamics via altered demographic rates due to changes in reproduction timing (Root et al. 2003, Dunn and Møller 2014), juvenile success (Stevenson and Bryant 2000), sex determination (Janzen 1994, Hawkes et al. 2007, Ospina-Álvarez and Piferrer 2008), and migration and seasonal cycles (Walther et al. 2002, Edwards and Richardson 2004). Decreasing populations sizes or extinctions that are attributed to climate change have been reported across taxa, including plants (Lenoir et al. 2008, Gottfried et al. 2012), amphibians (Pounds et al. 1999), reptiles (Erasmus et al. 2002, Sinervo et al. 2010), birds (Peterson et al. 2002, Jetz et al. 2007), corals (Carpenter et al. 2008), insects (Beaumont and Hughes 2002, Erasmus et al. 2002), and mammals (Moritz et al. 2008, Molnár et al. 2010). For example, climate change has affected populations of the alpine chipmunk *Tamias alpinus* by reducing genetic variability, due to habitat fragmentation and changes in local selection regimes, and this has manifested by decreasing overall population size (Rubidge et al. 2012).

Changes in species' population sizes will result in altered community structure (Walther 2010). At the extreme, this can lead to shifts in community states, such as from tropical rainforest to seasonal forests or savannas in the Amazon (Malhi et al. 2009, Staver et al. 2011), from coral to macroalgal cover in Caribbean reef systems (Mumby et al. 2007), or even the deforestation of temperate kelp forests and seagrass beds as tropical herbivores undergo range shifts (Vergés et al. 2014). There is evidence that climate change has already driven dramatic shifts in community composition worldwide. For example, in a rocky intertidal community on the U.S. West Coast, Barry et al. (1995) found that more than 70% of invertebrate species experienced significant changes in abundance between the 1930s and 1990s. Changes in

abundances were linked to geographical distributions and consistent with expectations of poleward shifts under climate change: At this site in central California, USA, southern species increased while northern species decreased in abundance. This link between geographic distributions and shifts in community composition suggests a role for the direct pathways of climate change, with altered individual physiology driving changes in population demography and sizes and, ultimately, leading to shifts in community composition.

Indirect effects of climate change

Decades of research have shown that both abiotic and biotic factors are important drivers of community structure. For example, competition for resources can shape community structure by altering growth, reproduction, and survival, leading to localized niche partitioning (Connell 1961, Tilman 1982). Similarly, predation can alter prey population sizes through both density- (Paine 1969, Kotler 1984) and trait (Werner 1991, Peckarsky et al. 2008)-mediated interactions. Positive species interactions also play an important role; facilitation can drive recruitment patterns, abundances and distributions, succession, and diversity by ameliorating harsh environmental conditions (Bertness and Callaway 1994, Bruno et al. 2003, Nicastro et al. 2012).

Abiotic factors can change the strength and direction of species interactions (Park 1962, Chamberlain et al. 2014, Roslin et al. 2017, Silliman and He 2018). For example, small fluctuations in seawater temperatures alter feeding rates in the ochre sea star *Pisaster ochraceus*, a keystone predator (Sanford 1999). These metabolic effects can lead to dramatic shifts in community structure, especially when they occur for strongly interacting organisms (Sanford 2002, Harley et al. 2006). Environmental conditions can also shift the outcomes and directions (negative vs. positive) of species interactions. In alpine communities, interactions between plants

shifted from competitive to facilitative at increased levels of elevation and environmental stress (Callaway et al. 2002). As climate change continues to alter existing environmental conditions, there will likely be dramatic shifts in community interaction webs.

The outcome of altered indirect effects depends to some degree on which species—such as predators as opposed to prey—are most strongly directly influenced by climate change, particularly if either guild contains species that drive community patterns. Altered demographic rates and distributions could lead to changes in predation intensity (Durant M. et al. 2007, Bascompte and Stouffer 2009, Freestone et al. 2011, Roslin et al. 2017), prey vulnerability (Kroeker et al. 2014), intraspecific competition due to predator or conspecific competitor release (Moorcroft et al. 2006, Gilman et al. 2010), and novel species interactions or spatial mismatch between associated species (Schweiger et al. 2008, Hegland et al. 2009, Potts et al. 2010). For example, sessile species are often better at acclimating to environmental stress than mobile species as they lack behavioral adaptations that allow them to avoid exposure (Van Kleunen and Fischer 2005, Petes et al. 2008). Similarly, species may be more or less vulnerable to environmental stress depending on their respective body sizes and behavioral adaptations (Menge et al. 2002, Vasseur and McCann 2005). Understanding how individual species or trophic guilds may respond to changing environmental conditions can help predict altered rates or importance of interactions and their effects on the community as a whole.

Incorporating biotic interactions

Both biotic and abiotic factors are important in structuring ecological communities. On a biogeographic scale, however, species interactions are thought to be less important in setting species distributions than the environmental conditions (Pearson and Dawson 2003). Because it

can be inappropriate to scale up localized processes to macroecological patterns, there is limited empirical evidence for broad-scale effects of biotic interactions (Araújo and Rozenfeld 2014). Incorporating biotic interactions into mathematical models, however, often provide a better predictive framework for species distributions across spatial scales. Such models have used different approaches to account for the strength of species interactions, including using co-occurrence (Araújo et al. 2011, Araújo and Rozenfeld 2014) shared phylogeny and evolutionary history (Morales-Castilla et al. 2017), and species' traits (Soberón 2007). However, widespread application of such models is challenging due to the difficulty of estimating the strength of species interactions across spatial scales (Araújo and Luoto 2007).

Community regulation models are existing frameworks that describe the role of both abiotic and biotic drivers in determining community structure and may be a useful tool for predicting the impacts of both of these drivers on species' distributions. The Menge–Sutherland model (1987; hereafter M–S) is one such framework that is ideal for incorporating both direct and indirect climate change effects. The M–S model describes the relative importance of abiotic and biotic drivers of species abundance distributions across environmental stress gradients. In areas where environmental stress is high, the importance of biotic interactions is likely to be low; conversely, biotic interactions are most important where there is low environmental stress. As a consumer stress model, M–S proposes that sensitivity to stress differs by trophic levels, with the lowest trophic levels most affected by predation and intermediate trophic levels affected by both biotic and abiotic stress. For example, in intertidal communities with high wave stress, sea stars can be excluded, leading to relatively low levels of predation (Menge 1992). Here, we build off of the M–S model to predict responses of predators and prey to climate change and test our predictions using a space-for-time substitution approach across a latitudinal gradient.

An intertidal case study: Testing the Menge–Sutherland model under climate change

To test the direct and indirect effects of climate change, we developed a conceptual model based on the M–S model, which describes the relative role of abiotic and biotic factors in driving community structure and diversity (Fig. 1). While climate change encompasses a broad range of abiotic conditions, we focused primarily on temperature, which plays a predominant role in setting species distribution patterns on broad and local scales and is projected to increase based on future climate change scenarios (Pearson and Dawson 2003).

In ecosystems with highly heterogeneous environments, slight changes in temperature are likely to have significant implications for local distribution patterns. Rocky intertidal ecosystems, where the M–S model was first applied, are an ideal system in which to test this model. These ecosystems are among the most physically stressful and dynamic: Along a vertical gradient in tidal emersion, the lower limits of species distributions are often controlled by biotic factors (predation and competition), while abiotic factors (temperature and desiccation) typically control the upper limits (Menge and Branch 2001, Harley 2011). These same abiotic and biotic stressors interact to set species latitudinal ranges, as environmental stress and community composition vary between biogeographic regions (Broitman et al. 2001, Blanchette et al. 2008).

As with the original description of the M–S model, we use responses of foundation species and keystone predators to project overall community-level patterns. Such species are important drivers of overall community structure because they both increase biodiversity, although through different mechanisms: Foundation species increase biodiversity through facilitation and resource provisioning (Dayton 1972), while keystone predators prevent

competitive exclusion by dominant species (Paine 1969). Impacts of climate change are likely to be amplified when they affect these leverage species (Harley et al. 2006).

Along the U.S. West Coast, the California mussel *Mytilus californianus* and the ochre sea star *Pisaster ochraceus* (hereafter, indicated by genus only) are the dominant foundation species and keystone predator, respectively (Paine 1969, Suchanek 1992). *Mytilus* is predominately distributed in the mid-intertidal zone, typically with its upper vertical limit set by limits of physiological tolerance to temperature and desiccation stress and its lower limit set by predation from *Pisaster* (Paine 1966, Suchanek 1978, Menge and Branch 2001). *Pisaster* has been shown to preferentially feed on *Mytilus* (Menge 1972), and its effects can be an order of magnitude higher than other intertidal predators (Navarrete and Menge 1996). It is also important to note that there is likely a reciprocal relationship between *Pisaster* and *Mytilus* in that lower limits of mussels could also determine foraging ranges of sea stars. *Pisaster* inhabits low intertidal and subtidal zones with the upper vertical limit also set by temperature and desiccation stress (Paine 1974, Monaco et al. 2015) Adult *Mytilus* are predominantly sessile, and must weather extreme temperatures in place, while *Pisaster* is highly mobile, allowing for behavioral thermoregulation (Broitman et al. 2009). These varying mechanisms allowing adaptation to environmental stress suggest that each species may respond differently to warming associated with climate change.

Our conceptual model illustrates two alternate hypotheses for the impacts of climate change on predation and, by extension, the distribution of foundational prey (Fig. 1). Increasing temperature could cause *Pisaster* predation to either increase or decrease, leading to a range contraction or downward range shift for *Mytilus*, respectively. Predation by *Pisaster* could increase if warming temperatures result in higher metabolic rates and compensatory increases in foraging (Sanford 1999, Pincebourde et al. 2008). Increased predation would likely drive a range

contraction for mussels, due to increasing environmental stress at the upper limits and increasing biotic stress (predation) at the lower limits. Because mussels increase habitat resources for associated invertebrate taxa (Suchanek 1992), any range contraction could by extension result in decreased biodiversity overall (Smith et al. 2006, Sorte et al. 2017). Conversely, if predation decreases due to increased stress-driven mortality (as predicted by consumer stress models; Menge and Sutherland 1976, 1987, Silliman and He 2018), *Mytilus* might be able to maintain its total elevation range by shifting both its upper and lower limit in tandem and, thus, maintain consistent levels of community diversity.

Methods

We applied our conceptual model to assess the direct and indirect impacts of increasing temperature on the distribution of foundation species in intertidal communities. Based on the M–S model prediction that predators are more strongly impacted by increasing environmental stress than prey, we hypothesized that temperature would drive community structure with (1) a direct effect on foundation species' upper vertical limits and (2) an indirect effect on foundation species' lower limits, via alterations in predators' upper vertical limits and densities, indicators of predation risk.

Surveys were conducted in summer and fall of 2016 and 2017 at 20 rocky intertidal sites spanning a thermal gradient along the U.S. West Coast (Fig. 2). At each site, we placed a 30-m horizontal transect parallel to the water line. Ten vertical transects were laid perpendicular to the horizontal transect at 3-m intervals. The vertical transects extended from 0 m MLLW (mean lower-low water) to the upper shore as indicated by absence of sessile organisms (i.e., bare rock). Along each vertical transect, we determined the tide height of the lowest (closest to the ocean)

and highest (closest to bare rock) *Mytilus* individuals within a 1-m belt (0.5 m on each side of the transect). Values were then averaged across transects to estimate the average lower and upper elevation limits of the mussel bed at the site level. Because sea stars are both rare and highly mobile, we quantified predation risk solely as a site-level metric. Over a 90-min search period, we identified all sea stars (*Pisaster*) within the survey area (30 m wide, vertically spanning from 0 MLLW to bare rock) and determined the tide height of each star (meters above MLLW) using a surveyor's laser level. At the site level, sea star distribution was decoupled from sea star density (linear regression, $P = 0.54$).

We used a space-for-time approach along a latitudinal gradient to test the direct effects of climate on predators and prey. Average yearly temperature across this gradient varies by $\sim 8^{\circ}\text{C}$, greater than the predicted end-of-century temperature increases of $1.5\text{--}4.5^{\circ}\text{C}$ in the warmest regions of our study (Cayan et al. 2008). Because temperature does not change linearly with latitude (Helmuth et al. 2006a), we used tidal predictions and air temperature data to characterize thermal conditions at each site across two temporal scales.

To characterize long-term thermal conditions affecting sessile foundation species (for which distributions are primarily determined by recruitment and post-settlement mortality), we quantified hourly temperatures at each site from the nearest land-based weather station for one year prior to the start of surveys using the *rwunderground* package (Shum 2017). Long-term hourly temperatures were cross-referenced with tidal predictions to focus on aerial temperatures during low tide. Because tidal amplitude varies across latitude, tide height data were converted to percent exposure time using tidal predictions from the preceding year ([tbone tides; http://tbone.biol.sc.edu/tide/](http://tbone.biol.sc.edu/tide/)). Seven low-tide long-term temperature metrics were calculated for each site from these hourly data: annual mean, annual 90th percentile, monthly mean, mean monthly

maximum, mean monthly range, mean daily maximum, and mean daily range (Appendix, Table S1). In the absence of a priori hypotheses for which of these metrics might be most important, and to account for collinearity among temperature variables, we used a principal components analysis to reduce the dimensionality of the temperature data. For long-term temperatures, PC1 was primarily driven by maximum temperature metrics (annual, monthly, and daily) and explained 86.7% of the variance. PC2 was driven by mean and range and explained 11.8% of the variance (Appendix, Fig. S1).

To quantify short-term temperatures affecting the intertidal distribution of sea stars, we placed two high-frequency temperature loggers (0.0083 Hz, iButtons, Maxim Integrated, San Jose, California, USA) in the mid-intertidal zone for 24 h spanning the predator and prey survey. Sea stars are highly mobile and respond behaviorally to thermal extremes, and feeding rates can be affected by changes in both aerial and sea surface temperatures (Szathmary et al. 2009). At each site, we measured mean, maximum, 90th percentile, and range of temperatures and used a principal components analysis to characterize acute thermal conditions. For short-term temperatures, PC1 was driven by maxima, while PC2 was comprised primarily of range and mean metrics. PC1 and PC2 accounted for 73.7% and 23.5% of the variation, respectively (Appendix, Fig. S1).

Multiple linear regression models were used to assess the correlations between average tide height distributions and hypothesized limiting factors—temperature (short- and long-term) and predation (average tide height and density)—across 20 sites. Residuals were visually inspected to ensure the data met normality assumptions. One site (Pyramid Point, California, USA; Appendix, Fig. S2) was identified as an outlier and was excluded from the analysis of upper

vertical limits. This location was dominated by boulders, and upper vertical limits were likely set by lack of available substrate and not indicative of absolute distribution limits.

We used structural equation modeling (SEM), informed by the results of the regression models, to test the strength and directionality of the linear relationships between species distributions and thermal stress. We predicted that long-term temperatures would have a negative direct effect on *Mytilus* ranges by decreasing the upper vertical limits, while short-term temperatures could have either a direct negative or positive effect on predation risk, leading to indirect effects on prey lower limits and ranges (Fig. 1). We tested direct and indirect effects models (where predation mediates temperature effects), based on the results of the multiple regression models.

Model estimates were based on maximum likelihood, and best fit was determined using chi-square indices. Model comparisons were made by using Akaike information criterion with an adjustment for small sample sizes (AIC_c) and comparing percentage of variation explained by each model. Data were analyzed using R v. 3.4.0 (R Core Team 2013). Structural equation models were fit using the lavaan package (Rosseel 2012) and AIC_c scores were calculated using the MuMIn package (Barton 2009). Data and code used for this study can be found at <https://github.com/piperw/CC-Direct-and-Indirect-Effects>.

Results

Multiple regression correlations

We found a direct negative relationship between long-term temperature and upper limits of mussels, as mussels did not extend as high on shore at warmer sites ($F = 9.20$, $P = 0.002$; Fig. 3; Appendix, Table S2). There was no effect of short-term temperatures ($F = 0.60$, $P = 0.56$;

Appendix, Fig. S3) on upper limits. Lower vertical limits of mussels were not significantly related to either long-term temperatures ($F = 0.34, P = 0.72$) or short-term temperatures ($F = 2.75, P = 0.09$). Although not statistically significant, sea star tide height showed a decreasing trend with short-term temperature ($F = 4.12, P = 0.06$) driven by PC2 ($t = 2.84, P = 0.02$). There was no relationship between sea star abundance and short-term temperature ($F = 0.08, P = 0.92$), and long-term temperature affected neither sea star distribution ($F = 0.40, P = 0.68$) nor abundance ($F = 2.42, P = 0.12$). When analyzing the effects of predators, we found a direct relationship between the lower vertical limits of mussels and predation risk ($F = 5.76, P = 0.03$), driven by mean sea star tide height ($t = 3.02, P = 0.02$). There was no effect of predation risk on the upper limits of mussels ($F = 3.15, P = 0.11$). term temperature. Mussel and sea star distributions are shown as percent exposure (the amount of the time a tide height is exposed to air). Dashed lines represent 95% confidence interval.

Direct and indirect pathways in structural equation models

The direct effects SEM (significant regression results) converged in 63 iterations ($\chi^2 = 0.21$), indicating an acceptable fit (Barrett 2007). Long-term temperature metrics were correlated with mussel upper limits (PC1: $z = 4.30, P < 0.0001$; PC2: $z = 1.87, P = 0.06$) and sea star density (PC1: $z = 2.70, P = 0.007$; PC2: $z = 1.97, P = 0.05$). There was also a significant relationship between mussel lower limits and average sea star tide heights ($z = 2.04, P = 0.04$), which were linked to short-term temperature metrics (PC1: $z = -1.37, P = 0.17$; PC2: $z = 2.38, P = 0.02$). Lower limits were not correlated with sea star density ($z = 1.13, P = 0.26$). Directionality of relationships was congruent between the multiple

regression models and the direct effects SEM, which explained 48.2% and 34.7% of the variation in mussel upper and lower limits, respectively (Appendix, Table S3).

When incorporating indirect pathways into the SEMs, significant indirect effects of temperature were observed in the model, which converged after 78 iterations ($\chi^2 = 0.13$). As in the direct effects model, long-term temperatures were directly correlated with mussel upper limits (PC1: $z = 4.39$, $P < 0.0001$; PC2: $z = 2.48$, $P = 0.01$) and sea star density (PC1: $z = 2.70$, $P = 0.07$; PC2: $z = 1.97$, $P = 0.05$). While sea star density significantly affected mussel lower limits ($z = 2.73$, $P = 0.006$), there was not an indirect effect of long-term temperatures (PC1: $z = -1.15$, $P = 0.25$; PC2: $z = -1.09$, $P = 0.28$). However, short-term temperatures did significantly affect lower limits of mussels when mediated by mean sea star tide height (PC1: $z = -2.62$, $P = 0.009$; PC2: $z = 3.36$, $P = 0.001$). The model explained 56.7% and 58.2% of the variation in mussel upper and lower limits (Fig. 4; Appendix, Table S4). height distributions of sea stars were assessed using structural equation models that compared the direct effects of temperature (top) to a model incorporating indirect effects (bottom). Standardized path coefficients (direction and magnitude) are included alongside paths. Dashed lines indicate indirect effects; asterisks indicate $P < 0.05$.

The indirect effects model was significantly better at predicting mussel upper and lower limits than the model incorporating only direct interactions ($\Delta AIC_c = 767.1$). For mussel distributions (mussel upper and lower limits), the indirect effects model explained, respectively, 8.2% and 23.3% more of the variation than the direct effects model (Table 1).

Discussion and Conclusions

We found that increased temperature was associated with a decrease in predation risk and that incorporating this indirect, biotic interaction led to predictions that explained approximately 18.8% more of the variance in prey distribution patterns across the U.S. West Coast. Our results were consistent with the hypothesis that environmental stress (temperature) sets the upper vertical limits of *M. californianus* and thus in accord with findings that intertidal organisms are often living at their thermal limits (Somero 2002). As temperatures rise during the coming century, these organisms may experience a depression in their upper limits, as higher tide heights become too environmentally stressful. At the same time, we found a strong relationship between predator distributions and lower vertical limits of mussel prey, and the vertical distribution of predators was itself altered by temperature. Interestingly, lower limits of mussels did not differ between sites with and without sea stars ($t = 0.21$, $P = 0.83$), suggesting that the effect of sea stars on mussels was related to their height on the shore but not their presence per se. Short-term (24 h) temperatures were correlated with the presence and location of sea star predators in these communities, which appear to play a role in controlling mussels' realized niche by setting their lower vertical limits. In our study, we found that at warmer sites, predation risk decreased rather than increasing. Thus, as climate change continues, effects of warming on predators may make thermal refuges (lower intertidal and subtidal habitats) more accessible, promoting local persistence of these critical foundation species.

Evidence for similar range shifts by intertidal mussels was observed in Argentinian Patagonia, where organisms experience similar temperatures to the U.S. West Coast but much greater desiccation stress (Bertness et al. 2006). In these communities, predation rate is relatively low, with native predators typically small in size and preferring to consume non-habitat forming

prey rather than foundation species (e.g., mussels) that ameliorate desiccation (Hidalgo et al. 2007). As physical stress increases along the U.S. West Coast, similar patterns may emerge, with predation at lower latitudes becoming less important in regulating species distributions and overall community structure. Furthermore, to the degree that a vertical shift is possible (and barring extreme sea level rise; Mengel et al. 2018), a downward range shift could conserve the relatively high levels of biodiversity associated with mussel beds. Mussel beds are one of the most diverse temperate ecosystems, harboring more than 300 species at a single site (Suchanek 1992, Smith et al. 2006).

Our study found that temperature drives distribution patterns of both sessile and mobile species across a broad thermal gradient. Rocky intertidal habitats have long been important study systems for considering impacts of climate change on range limits as many species are already living at their thermal limits (Tomanek and Somero 1999, Somero 2002). Species interactions are context-dependent, and within invertebrate-dominated communities, changes in temperature can lead to shifts in range boundaries due to changes in rates of predation or competition (Wetthey 1983, Sanford 2002). While our study used a space-for-time approach to evaluate likely impacts of increasing temperatures, other studies in the same system have also used historical comparisons. For example, Harley (2011) conducted both a space-for-time and time series study of intertidal zonation patterns in the Salish Sea. Results derived from both approaches indicated that the upper limits of mussels and barnacles shift downward under warmer conditions (including comparing contemporary distributions to those recorded in 1957–1958). Contrary to our results, no accompanying change was observed for lower vertical limits of these prey species, and sea star foraging (upper) limits were not correlated with temperature in the space-for-time study (no sea star data were available for historical comparisons; Harley 2011).

A contributing factor to the sea star density patterns documented in our study (but not Harley 2011) is coast-wide declines in sea star populations due to an unprecedented epidemic of sea star wasting disease (SSWD; Hewson et al. 2014). The disease appears to be caused by a densovirus whose epidemiology is triggered by increases in sea surface temperature (Eisenlord et al. 2016). This epidemic amplified the pre-existing gradient in predation pressure from north to south. Although prior to the epidemic, sea star abundance increased with latitude, sea stars were absent (or occurred only subtidally) in southern locations after the epidemic, and predation rates declined drastically at all sites (Menge et al. 2016). Although a direct link between SSWD and temperature has yet to be confirmed, the outbreak and its consequences for these keystone predators highlight additional indirect avenues for climate change to alter species interactions and the surrounding community.

In the face of rapidly shifting ecological communities, space-for time surveys are likely to become an increasingly important predictive approach for researchers and conservationists. Such studies have advantages in allowing us to evaluate patterns across a range of temperatures or environmental conditions (Freestone et al. 2011, Roslin et al. 2017) that would require decades or more in a longitudinal study (Pickett 1989). There are undoubtedly drawbacks, including that multiple abiotic and biotic factors can co-vary across broad gradients (Friedlander and DeMartini 2002, Pennings and Silliman 2005) and strictly linear/parallel gradients are rare. However, in the absence of historical baselines for populations of interest, quantification of the strength of species interactions across environmental gradients can be a useful tool for identifying vulnerable species and communities as climate change exacerbates already stressful conditions.

Although our expansion of the Menge–Sutherland model was applied here to predict impacts of climate change on a key predator–prey interaction in intertidal ecosystems, we intend for this application to show that community regulation models may be a useful tool for developing and testing predictions of how communities will respond to climate change. Although ecologists widely recognize that biotic interactions—facilitation, competition, or predation—can drive population sizes of associated species (Schoener 1983, McNamara and Houston 1987, Case and Taper 2000, Bruno et al. 2003), the majority of climate change forecasting models include only abiotic variables. Classic community regulation models, such as the Menge–Sutherland model (1976, 1987), explicitly incorporate species interactions and can provide a useful starting point for considering the cascading community-level effects of climate change.

Incorporating species interactions into models of future species' distributions can significantly improve explanatory and predictive power (Araújo and Luoto 2007); however, there are understandably limitations to applying these models. Idiosyncratic species (McKinney 1997, Perry et al. 2005, Helmuth et al. 2006, Møller et al. 2008) and population responses (Stillman 2003, Aitken et al. 2008, Sorte et al. 2011) are expected under climate change, which can add uncertainty to model parameters. Interacting species often do not undergo range shifts in unison (Harley 2011), which could lead to the exclusion of some species in a community if they are unable to keep pace. Additionally, these models do not include larger scale (e.g., meta-population) dynamics (Menge and Olson 1990), community shifts due to disturbance (Jurgens et al. 2017) or direct human impacts, such as deforestation or habitat fragmentation. More complex community regulation models would be required to account for the effects of multiple environmental stressors, which themselves can have interactive ecological effects. For example,

elevated nutrients and decreased pH have a synergistic effect, accelerating the growth of filamentous algae beyond the expected impacts of either stressor alone (Russell et al. 2009).

However, these responses can be unpredictable. In a synthesis of 171 marine systems, Crain et al. (2008) found that in experiments where two or more climate stressors were manipulated, responses were 26% additive, 36% synergistic, and 38% antagonistic. Moreover, interactions varied by level of biological organization (e.g., individual, population, community) and the type and number of stressors (Crain et al. 2008). Still, adapted community regulation models can provide important context for climate change responses, especially for species with critical roles in their community, such as foundation species, keystone predators, or ecosystem engineers.

Unfortunately, the roles of many species in their communities are still not well understood and predicting how species interactions are likely to shift may be difficult if little is known about how the community is currently regulated. Additionally, novel species interactions are now occurring as species' ranges shift in response to climate change (Walther et al. 2002, Parmesan 2006). While range shifts can ameliorate increasingly stressful environments, species undergoing range shifts are not moving into unoccupied habitats and may have unanticipated effects on a new community (and vice versa). As species move into new communities, they can have ecological advantages over endemic species due to the lack of a shared evolutionary history. This can manifest through release from predators and competitors, as well as increased predation success due to naïve prey. Climate change may lead to the development of consumer fronts, shifts of predators due to resource depletion (Silliman et al. 2013), and altered species distributions and community interactions can result in increased fluctuations in species population sizes as communities adjust to structural changes (Boulangeat et al. 2018). Few

studies have examined the community-level impacts of species range shifts, which can influence recipient communities to the same degree as non-native species invasions (Sorte et al. 2010).

Our study focused on the context dependency of species interactions across a broad thermal gradient. Interestingly, our results were contrary to Silliman and He (2018) who found that physical stress had additive effects on consumer control, suggesting that reduced top-down control is only one potential outcome. Similarly, facilitation could also increase under climate change having an overall positive effect on a community (Silliman et al. 2015). Understanding how changes to physical stress lead to altered strength and directionality of species interactions is an important next step for incorporating indirect effects into climate change projections. Existing frameworks have considered trait matching or phylogeny as proxies for future biotic interactions (Morales-Castilla et al. 2015, Brousseau et al. 2018), while others have found that ecosystem type or predator thermoregulation has an important effect (Silliman and He 2018).

Here, we present an alternative method based on established community regulation models, which can be adapted for use in many ecological communities without requiring extensive knowledge of all existing species interactions. We anticipate that this tool could be particularly useful for managers and conservationists looking to understand the threat of climate change for species that have profound impacts on communities, such as ecosystem engineers or foundation species. Incorporating the direct physiological effects as well as indirect effects via changes in species interactions as a result of global and regional climate could provide a useful framework for predicting outcomes and assisting in prioritization of management and conservation strategies. In the face of unprecedented change to ecological populations, communities, and ecosystems, models must adapt as well.

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Tables

Table 1. AICc scores and percent of variation of mussel upper and lower limits explained by the direct and indirect structural equation models (See Figure 4).

Model	AICc Score	Upper Limits	Lower Limits
Direct Effects	1159.6	48.5	34.9
Indirect Effects	392.5	56.7	58.2
Difference	767.1	8.2	23.3

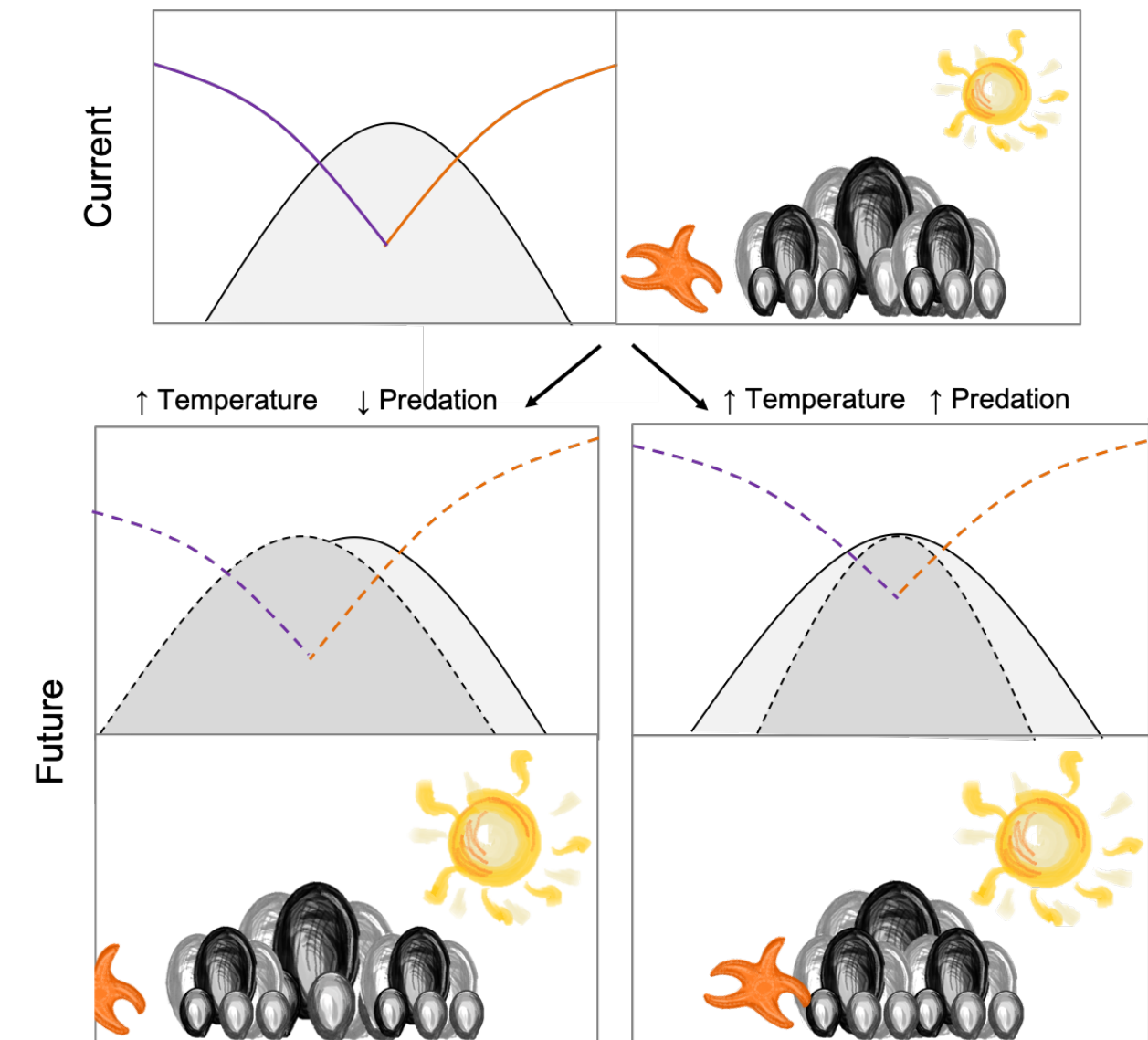


Figure 1. Conceptual diagram of climate change impacts on community structure in a rocky intertidal community. Temperature (orange) and predation stress (purple) are expected to set vertical distributions of prey (gray). As the climate changes, temperatures will increase while predation may either decrease (left) or increase (right), leading to downward range shifts or range contractions of prey species.

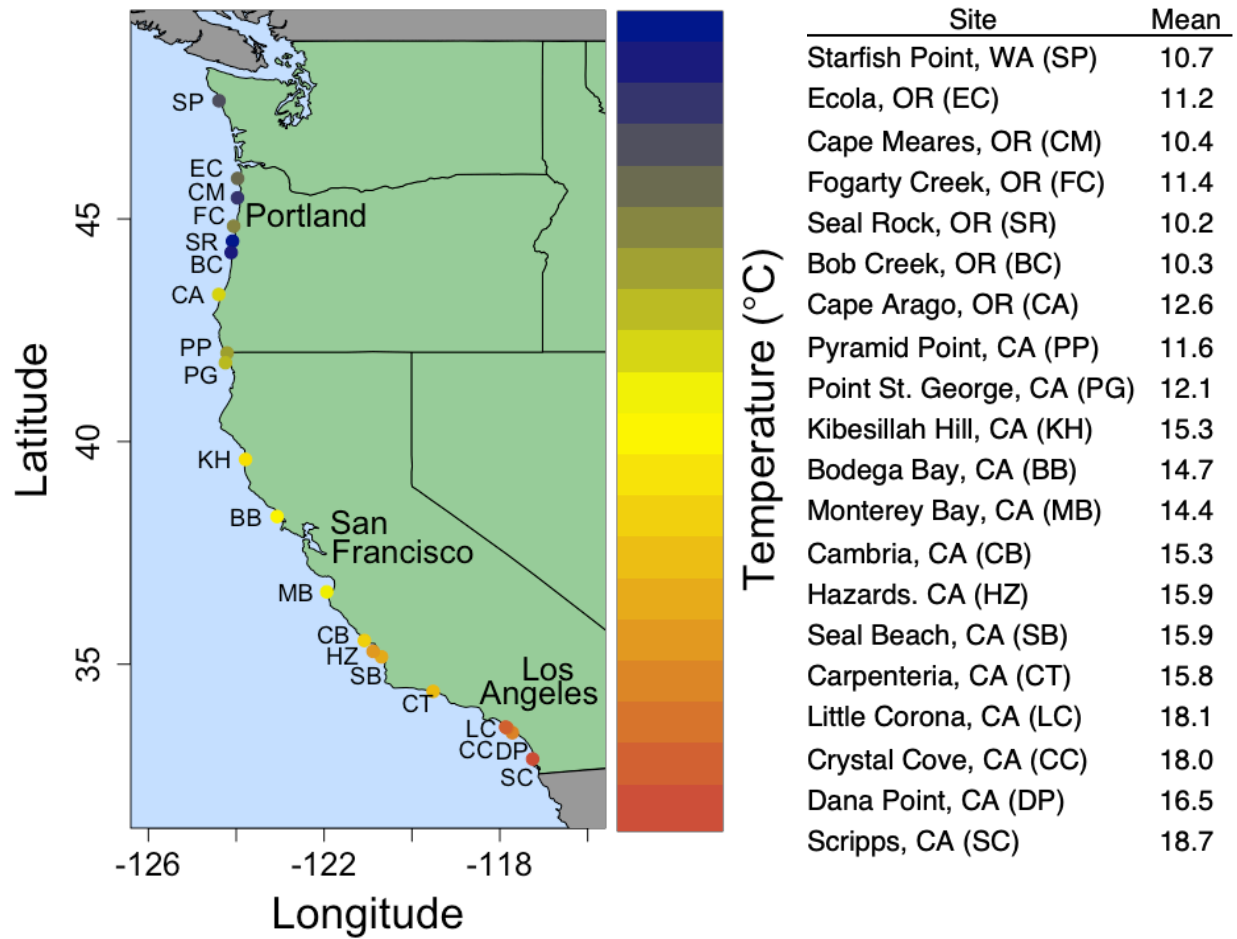


Figure 2. Locations of study sites along the U.S. West Coast. Color codes represent the mean annual temperature at each site (Mean), as temperature is not directly correlated with latitude in this system. For a full list of all temperature metrics, see Table S1.

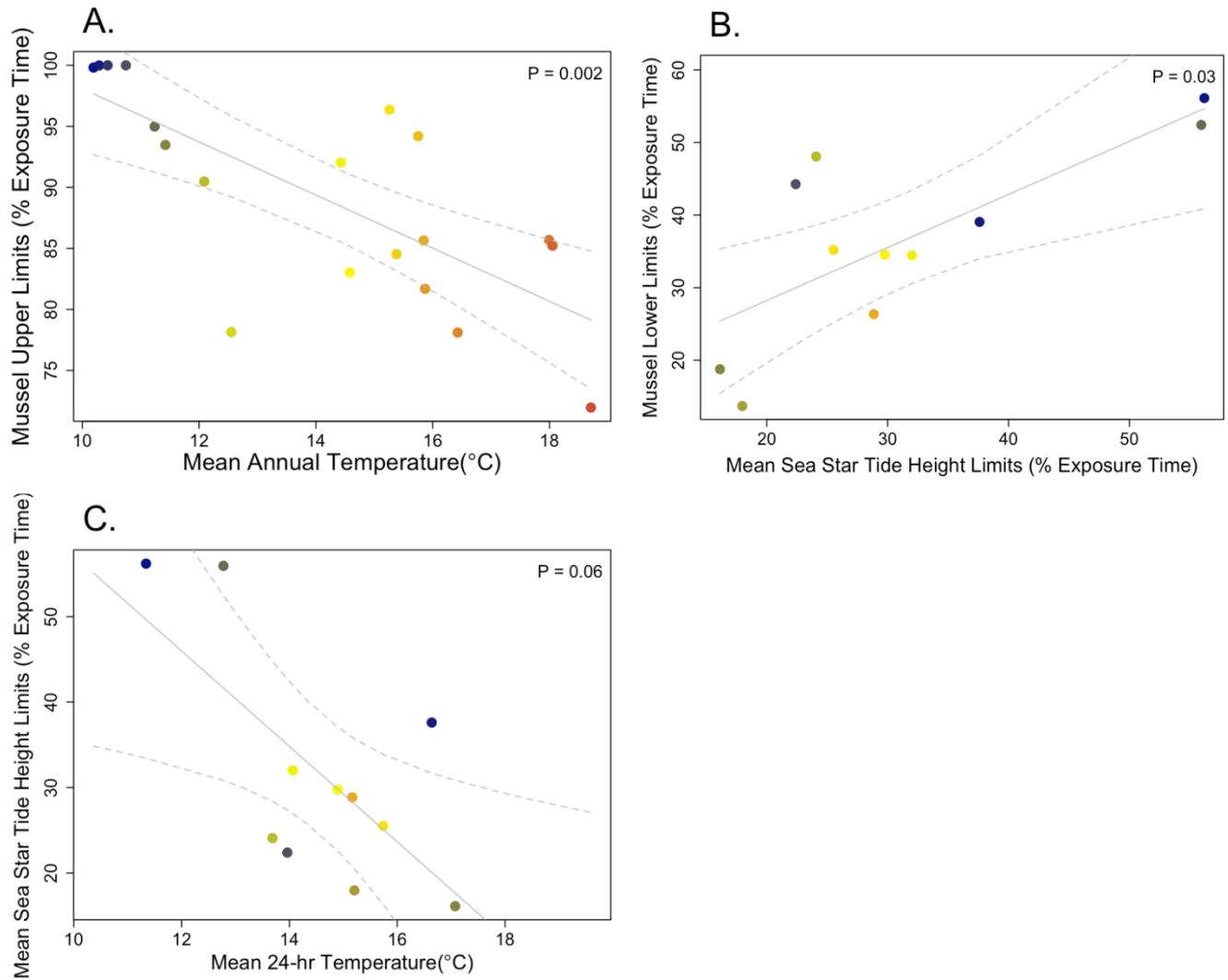


Figure 3. Multiple regression models were used to assess the relationship between A) average upper limits of mussel distributions and long-term temperature, B) average lower limits of mussel distributions and average sea star distributions, and C) average sea star tide heights and short-term temperature. Mussel and sea star distributions are shown as percent exposure (the amount of the time a tide height is exposed to air). Dashed lines represent 95% CI.

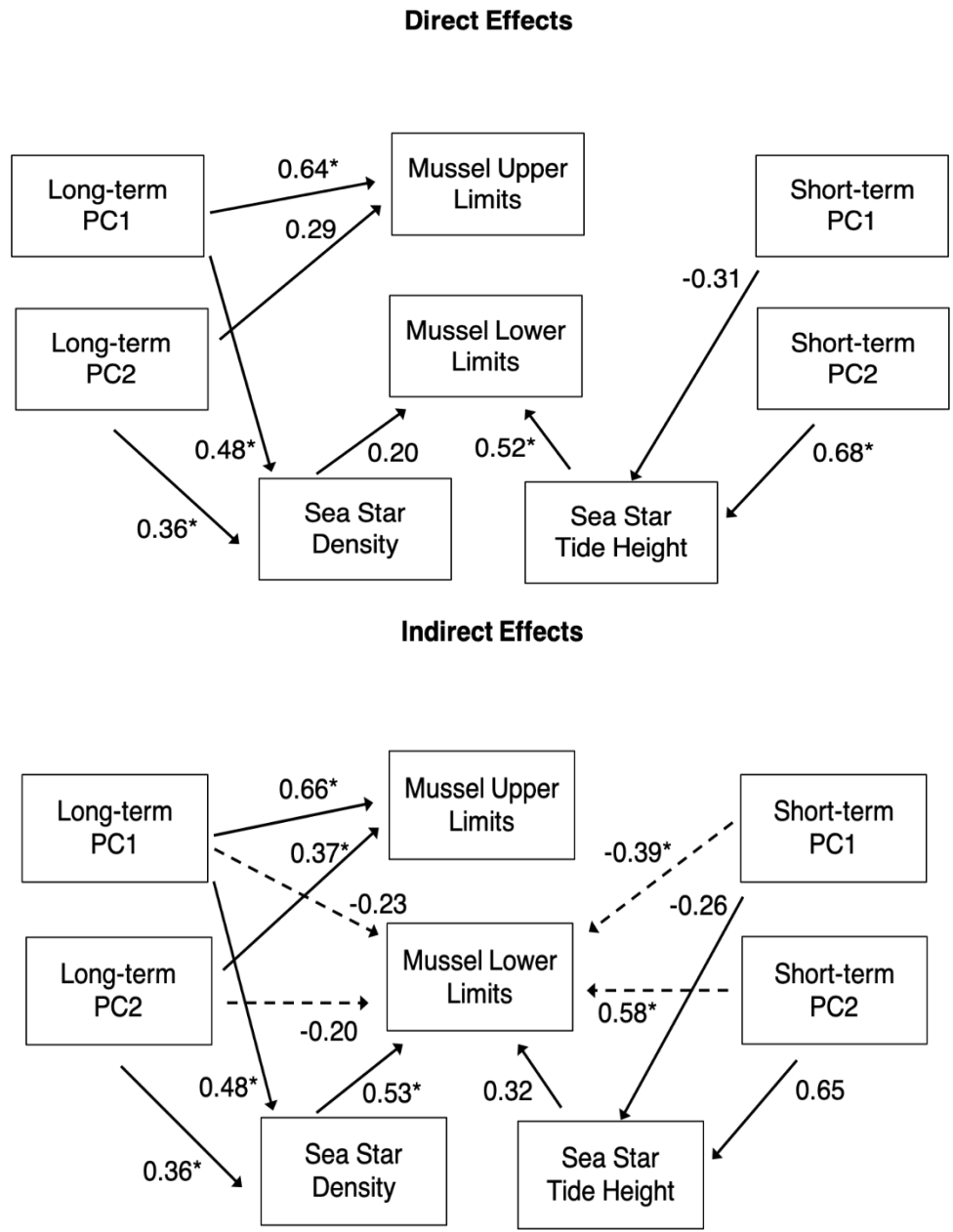


Figure 4. The effects of temperature on upper and lower limits of mussels and average height distributions of sea stars were assessed using structural equation models that compared the direct effects of temperature (top) to a model incorporating indirect effects (bottom). Standardized path coefficients (direction and magnitude) are included alongside paths. Dashed lines indicate indirect effects, asterisks indicate $P < 0.05$.

Table S1. Summary statistics of long- and short-term temperature metrics at each study site from north to south. Long-term temperature metrics are annual mean (Mean), 90th percentile (90th), monthly mean (MM), mean monthly maximum (MMM), mean monthly range (MMR), mean daily maximum (MDM), and mean daily range (MDR). Short-term temperature metrics are mean (ST Mean) 90th percentile (ST 90th), maximum (ST Max), and range (ST Range).

Site	Latitude	Mean	90 th	MM	MMM	MMR	MDM	MDR	ST Mean	ST 90 th	ST Max	ST Range
SP	47.65298	10.7	16.1	10.9	21.5	19.1	13.4	5.4	14.0	19.3	22.25	14
EC	45.90812	11.2	17.8	11.3	22.1	18.3	14.1	6.1	12.8	22.0	32.25	23.5
CM	45.47200	10.4	17.0	10.7	23.0	21.7	14.9	8.0	13.0	15.5	22	13.5
FC	44.83739	11.4	16.0	11.3	19.9	16.1	13.6	4.8	17.1	20.5	22.25	9.75
SR	44.49998	10.2	15.0	10.4	19.7	16.2	12.7	5.1	11.3	13.5	16	5.5
BC	44.24510	10.3	15.6	10.4	19.8	16.3	13.0	5.5	16.6	16.6	28.25	17.25
CA	43.30266	12.6	17.7	12.6	21.9	16.5	15.5	6.0	10.4	13.6	24.25	16
PP	41.98888	11.6	17.2	11.9	24.4	19.6	14.5	5.7	15.2	23.0	29.25	17.75
PG	41.77040	12.1	15.6	12.2	19.4	13.9	14.5	4.9	13.7	15.5	19.25	7.25
KH	39.59916	15.3	28.3	15.4	31.6	27.9	22.3	13.4	15.7	23.0	24.75	14
BB	38.31655	14.7	25.0	15.0	30.2	25.5	22.7	14.2	14.9	30.0	34.5	26
MB	36.62490	14.4	19.4	14.4	25.4	17.8	18.5	7.4	14.1	16.0	18.25	5.25
CB	35.53278	15.3	27.2	15.4	32.2	29.6	24.8	17.1	14.3	14.3	18.5	6.75
HZ	35.28939	15.9	23.3	16.2	30.5	24.1	22.7	11.8	13.2	15.0	21	10.75
SB	35.16499	15.9	23.3	15.9	29.9	23.4	22.3	11.2	15.2	15.2	17	5.5
CT	34.38886	15.8	21.7	16.0	28.4	21.6	21.2	10.4	18.5	18.5	37	23.25
LC	33.58927	18.1	24.4	18.3	30.1	20.6	22.8	8.6	17.8	23.1	29.5	16
CC	33.56885	18.0	24.4	18.3	30.4	20.9	22.7	8.7	18.4	22.5	26.75	11
DP	33.46162	16.5	23.9	16.6	29.9	23.7	21.7	10.3	18.0	21.0	25.5	10.75
SC	32.87115	18.7	25.6	18.9	31.7	21.8	23.7	9.1	19.6	19.6	28	11.5

Table S2. Summary of results of multiple regression models of the effects of A) long-term temperature and B) short-term temperature on the average upper and lower limits of mussels, average sea star tide height, and sea star density, as well as C) predation risk on average mussel maxima and minima. Significant values ($p < 0.05$) are indicated in bold.

A.

Parameter	PC1		PC2		Overall Model			
	t	P	t	P	R ²	df	F	P
Mussel Upper Limits	3.66	0.002	2.28	0.04	0.53	18	9.20	0.002
Mussel Lower Limits	0.64	0.53	-0.51	0.62	0.04	19	0.34	0.72
Sea Star Tide Height	0.87	0.41	0.64	0.54	0.09	10	0.40	0.68
Sea Star Density	1.96	0.07	1.01	0.33	0.22	19	2.42	0.12

B.

Parameter	PC1		PC2		Overall Model			
	t	P	t	P	R ²	df	F	P
Mussel Upper Limits	-0.34	0.74	1.03	0.32	0.07	18	0.60	0.56
Mussel Lower Limits	-1.42	0.18	1.87	0.08	0.24	19	2.75	0.09
Sea Star Tide Height	-1.77	0.11	2.84	0.02	0.51	10	4.12	0.06
Sea Star Density	0.29	0.77	0.27	0.79	0.01	19	0.08	0.92

C.

Parameter	Star Height		Star Density		Overall Model			
	t	P	t	P	R ²	df	F	P
Mussel Upper Limits	0.74	0.48	2.26	0.06	0.47	9	3.15	0.11
Mussel Lower Limits	3.02	0.02	0.85	0.42	0.59	10	5.76	0.03

Table S3. Parameter estimates and variance-covariance matrix of the direct effects structural equation model. Significant values ($p < 0.05$) are indicated in bold.

Regression		B	SE	z	P	β
Mussel Upper Limits	~ Long-term PC1	2.26	0.53	4.3	< 0.001	0.64
	~ Long-term PC2	1.98	1.06	1.87	0.06	0.29
Mussel Lower Limits	~ Sea Star Tide Height	0.48	0.24	2.04	0.04	0.51
	~ Sea Star Density	0.06	0.05	1.13	0.26	0.20
Sea Star Tide Height	~ Short-term PC1	-2.60	1.9	-1.37	0.17	-0.31
	~ Short-term PC2	10.27	4.32	2.38	0.02	0.68
Sea Star Density	~ Long-term PC1	10.09	3.74	2.7	0.01	0.48
	~ Long-term PC2	14.38	7.24	1.99	0.05	0.36

	Upper Limits	Lower Limits	Star Height	Star Density	LT PC1	LT PC2	ST PC1	ST PC2
Mussel Upper Limits	59.52	179.45						
Mussel Lower Limits	9.47	106.00						
Sea Star Tide Height	32.37	195.55	200.88					
Sea Star Density	142.54	8.79	156.32	2048.91				
Long-term PC1	10.61	2.08	12.47	47.34	4.69			
Long-term PC2	2.47	2.08	2.13	18.00	0.00	1.25		
Short-term PC1	-2.14	-4.10	-7.27	-10.19	-0.85	-0.11	2.80	
Short-term PC2	2.61	5.15	9.15	12.65	1.00	0.18	0.00	0.89

Table S4. Parameter estimates and variance-covariance matrix of the indirect effects structural equation model.

Regression		B	SE	z	P	β
Mussel Upper Limits	~ Long-term PC1	2.50	0.57	4.39	< 0.001	0.66
	~ Long-term PC2	2.73	1.10	2.48	0.01	0.37
Mussel Lower Limits	~ Sea Star Tide Height	0.33	0.33	0.99	0.32	0.32
	~ Sea Star Density	0.17	0.06	2.73	0.01	0.53
	~ Long-term PC1	-3.38	1.29	-2.62	0.01	-0.39
	~ Long-term PC2	8.77	2.61	3.36	< 0.001	0.58
	~ Short-term PC1	-1.54	1.35	-1.15	0.25	-0.23
	~ Short-term PC2	-2.52	2.32	-1.09	0.28	-0.20
	~ Short-term PC1	-2.56	1.41	-1.81	0.07	-0.30
Sea Star Tide Height	~ Short-term PC2	5.49	3.80	1.44	0.15	0.36
	~ Long-term PC1	-3.25	1.49	-2.18	0.03	-0.49
Sea Star Density	~ Long-term PC2	-4.95	2.20	-2.25	0.02	-0.38

	Upper Limits	Lower Limits	Star Height	Star Density	LT PC1	LT PC2	ST PC1	ST PC2
Mussel Upper Limits	68.08							
Mussel Lower Limits	-19.75	207.22						
Sea Star Tide Height	36.12	106.89	195.41					
Sea Star Density	167.36	248.24	152.90	2048.91				
Long-term PC1	11.72	4.39	12.19	47.34	4.69			
Long-term PC2	3.42	-1.21	2.02	18.00	0.00	1.25		
Short-term PC1	-2.43	-7.85	-7.04	-10.19	-0.85	-0.11	2.80	
Short-term PC2	2.98	5.83	8.87	12.65	1.00	0.18	0.00	0.89

Figure S1. Principle components analyses were used to reduce the dimensionality of temperature metrics. For both A) long-term temperature and B) short-term temperature, PC1 was driven by maximum temperatures and explained 86.7% and 73.7% of the data, respectively. PC2 was driven by mean and range metrics and explained 11.8% and 23.5% of the data.

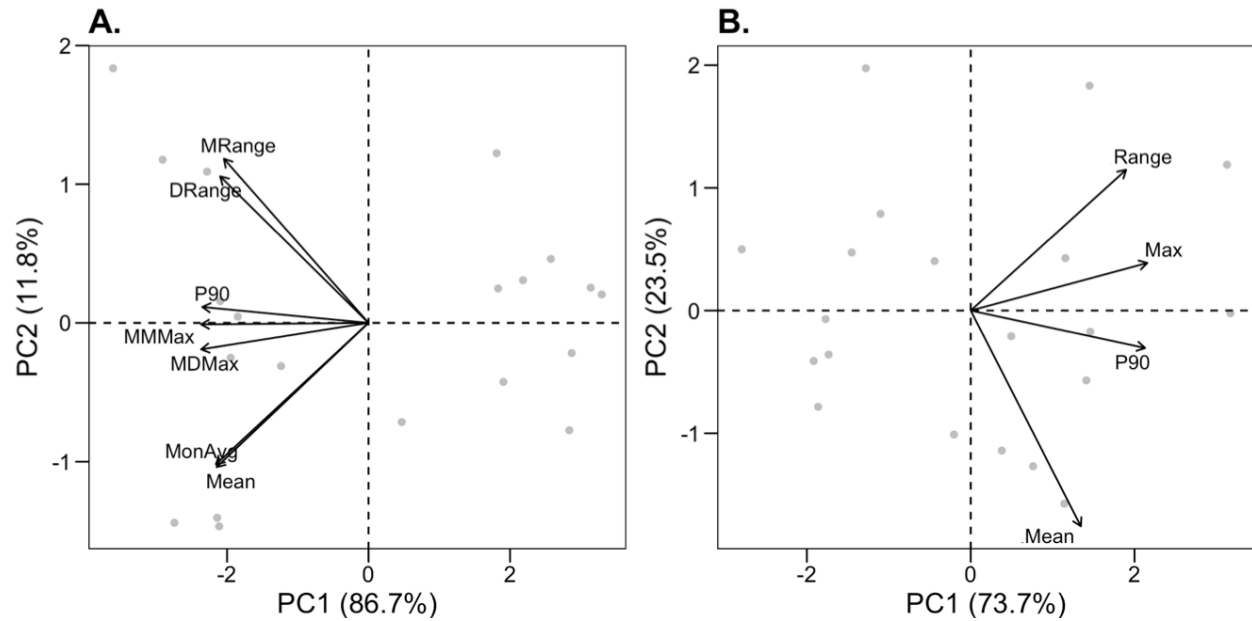


Figure S2. Pyramid Point, CA (PP) was excluded from the analysis of upper vertical limits as an outlier. PP was excluded based on A) visual observations of the regression, B) the non-normality of model residuals, C) the occurrence of PP more than 1.5 interquartile ranges below the first quartile, and D) visual assessments of site photos. PP is identified by the open circles in each plot. Because this location was dominated by boulders, upper vertical limits were likely due to lack of available substrate and not physiological limits.

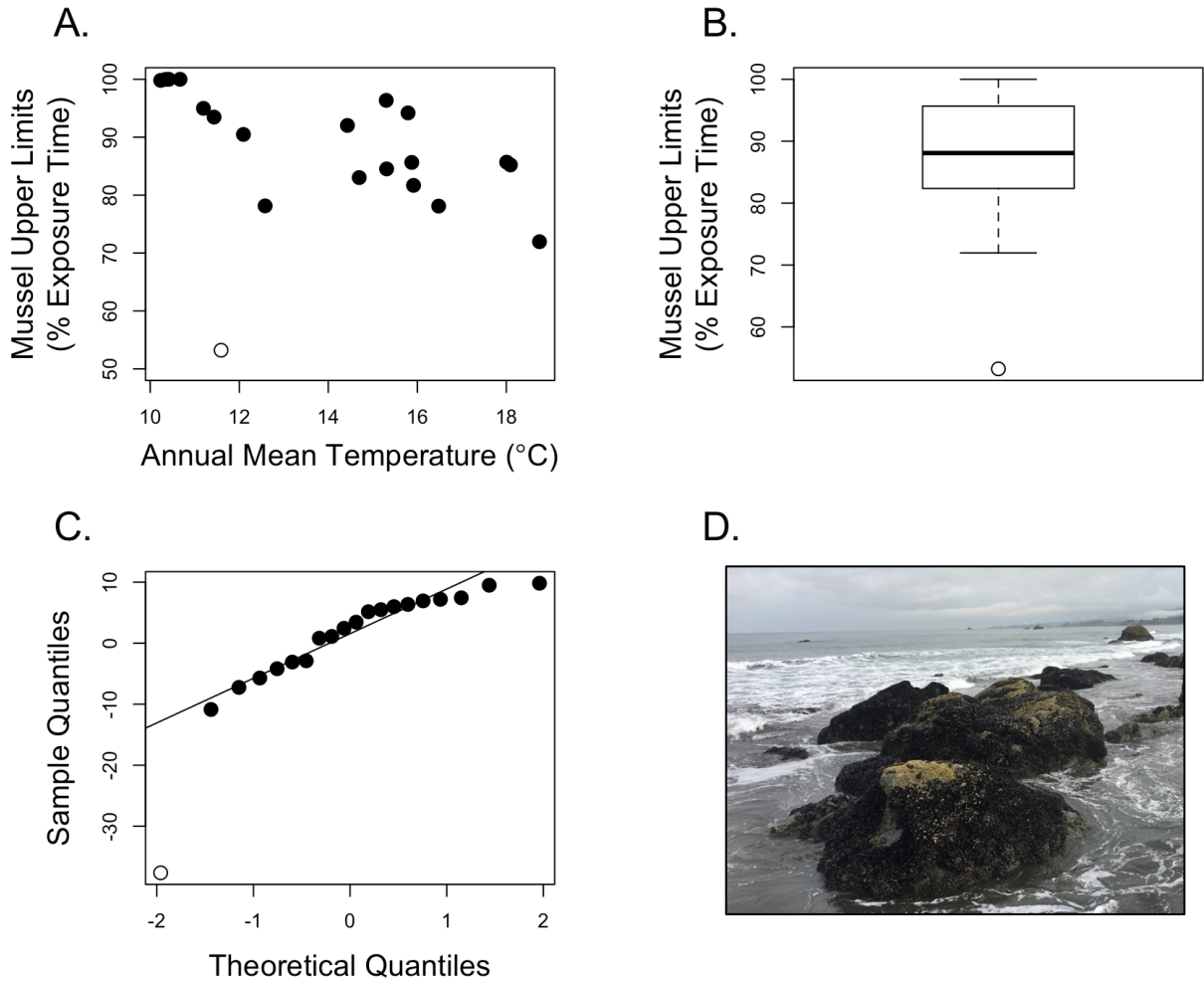
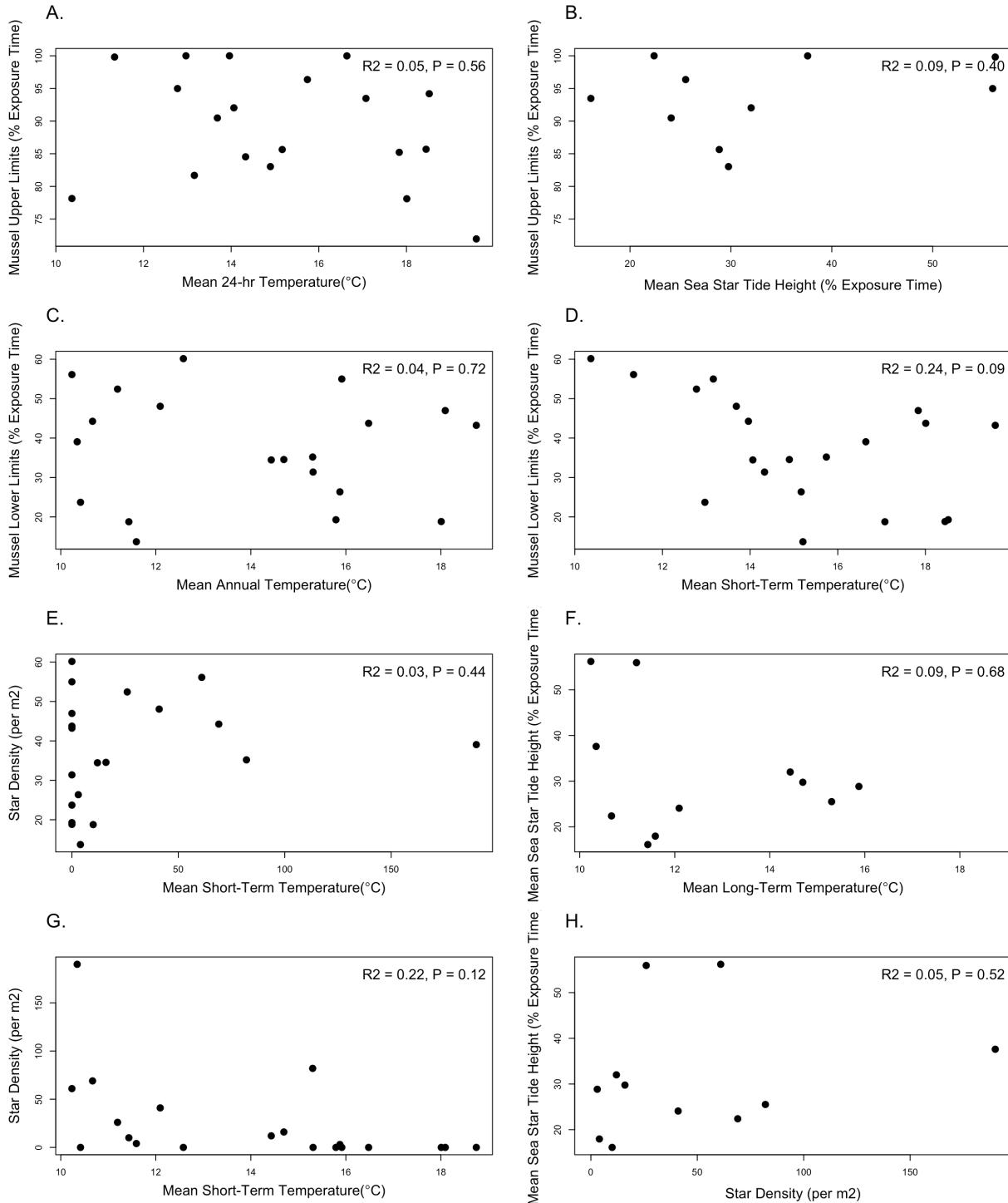


Figure S3. There was no effect of either A) short-term temperature or B) mean sea star tide heights on the average upper limits of mussels. Additionally, there was no relationship between mussel lower limits and either C) long- or short-term temperature D). Neither E) sea star density nor F) mean sea star tide heights were related to long-term temperature, and sea star density was not correlated with G) short-term temperature. There was no effect of H) sea star density on average sea star tide height.



CHAPTER 2

Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts

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Abstract

As Earth's climate rapidly changes, species range shifts are considered key to species persistence. However, some range-shifting species will alter community structure and ecosystem processes. By adapting existing invasion risk assessment frameworks, we can identify characteristics shared with high-impact introductions and thus predict potential impacts. There are fundamental differences between introduced and range-shifting species, primarily shared evolutionary histories between range shifters and their new community. Nevertheless, impacts can occur via analogous mechanisms, such as wide dispersal, community disturbance and low biotic resistance. As ranges shift in response to climate change, we have an opportunity to develop plans to facilitate advantageous movements and limit those that are problematic.

Introduction

Anthropogenic climate change is increasingly affecting species and ecosystems across the globe, threatening biodiversity at both local and broad scales (Field et al. 2014). In response, species from many taxonomic groups and ecosystems are undergoing redistribution towards higher latitudes and elevations due to both the direct (for example, physical limitations) and indirect (for example, altered species interactions) effects of climate change (Parmesan and Yohe 2003, Sorte et al. 2010, Chen et al. 2011, Pecl et al. 2017, Lipton et al. 2018). Because colonizing new habitats helps species persist both regionally and globally (Hoegh-Guldberg and others 2008, Dawson et al. 2011), range shifts are seen as overwhelmingly beneficial to biodiversity conservation⁹. With the exception of some problematic species (for example, forest pests, Nackley et al. 2017), as well as translocations and assisted migrations (McLachlan et al. 2007, Hargreaves et al. 2014, Bonebrake et al. 2018), few studies (although see Sorte et al. 2010

for an example) have assessed the community and ecosystem impacts of species tracking their climate niche into new areas. This research gap remains despite theoretical literature that recognizes the potential for impacts and the need for such research (Gilman et al. 2010, Harley 2011, Post 2013, Wallingford and Sorte 2019). The lack of studies on range shift impacts is surprising given that the introduction and spread of new species is often viewed by ecologists through the lens of invasion biology, where the primary concern is the potential for negative impacts on the recipient community. This dichotomy underscores the importance of considering the ecological impacts of range-shifting species in terms of both the benefits, particularly to their persistence, as well as the potential costs to recipient communities and ecosystem processes.

There are important ecological differences between introduced and range-shifting species (see Table 1 for definitions) that result in different levels of risk. For example, synthesis work considering a broad range of introduced species suggests that 10–50% become invasive and have negative impacts (Williamson and Fitter 1996, Jeschke and Strayer 2005, Simberloff et al. 2012). In contrast, results from analyses of range shift impacts are mixed, with some showing magnitudes of impacts similar to introduced species³ and others indicating that native species are less likely to be problematic when shifting to nearby recipient communities (Simberloff et al. 2012). Potential differences in impact could be driven by range shifters' shared evolutionary history with some species in the recipient community; however, understanding which species are likely to have a large negative impact is critical for conservation of species in the many communities globally that are being joined by range shifters. Invasion ecology, therefore, provides insight for considering these interactions and assessing risk on a species-by-species basis.

The movement of populations in response to climate change is, in many ways, similar to the invasion of introduced species: it creates the potential for novel species interactions (Gilman et al. 2010). Both introduced and range-shifting species have been shown to impact recipient communities by consuming, parasitizing or competing with native species that lack the ability or defenses to overcome them (Sorte et al. 2010, Naeem et al. 2017). Nevertheless, range shifters frequently share an evolutionary history with some species in the recipient community, so interactions will not be completely novel, decreasing their potential for harmful impacts due to established niches and community roles (Keane and Crawley 2002). As more species shift in response to climate change, methods for assessing potential impacts on recipient communities, and thus prioritizing which species to facilitate, become more valuable. Here, we leverage our understanding of biological invasions to describe a framework for assessing the likelihood and degree to which range shifters could impact recipient communities.

Assessing the impacts of climate-driven range shifts

Invasion ecologists have invested considerable effort in developing rubrics for predicting which introduced species are likely to become problematic (Pyšek and Richardson 2008). Catford et al. (2009) proposed a holistic framework that broadly grouped these hypotheses into categories of propagule pressure, abiotic characteristics of the recipient community and biotic characteristics of both the recipient community and introduced species. Many (but not all) of the factors influencing invasion success, as identified in the Catford et al. framework, might also translate to impacts of range-shifting species. We can, therefore, use this framework to help assess the potential impacts of range shifters as well as to identify vulnerable recipient communities (Fig. 1).

Propagule pressure

Propagule or dispersal pressure is critical to the establishment of any introduced species (Colautti et al. 2006, Leung et al. 2012). Most invasive species experience a lag period between the initial introduction and the time at which they become invasive. This lag can last from 3–140 years in plants and 10–38 years in birds (Coutts et al. 2018), and is attributed to a founder effect of the initial established population. Increased propagule pressure can reduce this lag time by increasing genetic diversity and adaptability of spreading populations (Lockwood et al. 2005, Ricciardi and Simberloff 2009). Unlike with introduced species, for which genetic diversity is strongly limited by propagule pressure and number of introduction events, propagules of range shifters are likely to have been arriving sporadically into the recipient community at locations near the range margin. Thus, the existence of nearby source populations of range shifters could reduce time lags and increase the rate of population growth and range expansion, especially for species that are prolific propagule producers (Szűcs et al. 2017, Fig. 1). For example, marine organisms are expanding by an order of magnitude faster than terrestrial species, likely due to higher connectivity between communities, which translates to fewer barriers to widespread dispersal (Sorte et al. 2010). Higher propagule pressure at range margins makes it more likely that a range-shifting species will establish and spread into a novel recipient ecosystem.

Abiotic effects on impacts

Introduced species can establish in new communities when they have a competitive advantage or they occupy an empty niche; for example, anthropogenic disturbances can provide a window of opportunity for non-natives (Dale et al. 2001). As the climate continues to change, recipient communities are likely to experience more frequent and acute abiotic stresses, which

might lead to decreased population sizes and extirpations (even extinctions) in these communities (Thomas 2010, Chen et al. 2011). This may enable the establishment of range shifters as they track their optimal climate conditions. For example, shorter winters and higher minimum temperatures are allowing many range-shifting insect pests (such as spruce and pine beetles) to colonize forests that were previously outside their ranges (Battisti et al. 2005, Raffa et al. 2013, Lesk et al. 2017), leading to profound impacts on these ecosystems (Dukes et al. 2009). As these fast-growing insect pests shift into novel forest communities, drought conditions increase trees' vulnerability and exacerbate the pests' impacts (Berg et al. 2006, Weed et al. 2013).

Similarly, some of the most problematic introduced woody plant species host nitrogen-fixing microorganisms in their roots, thus allowing them to outcompete native species in an otherwise stressful, low-nutrient environment. *Myrica faya* in Hawaii, *Lupinus arboreus* in California grasslands and *Acacia* spp. in South Africa are examples of highly invasive shrubs and trees that benefit from greater access to nitrogen in nitrogen-poor soils (Rice et al. 2004). Black locust (*Robinia pseudoacacia*) is a fast-growing, nitrogen-fixing native tree of southeastern North America that is currently undergoing a climate-mediated range shift (McCarthy-Neumann and Ibáñez 2012). As black locust moves north of its current range in response to climate change (Iverson et al. 2008), it is likely to have a competitive advantage over native vegetation, especially in nitrogen-deficient soils. Thus, recipient ecosystems that are heavily disturbed or have low nutrient availability may incur larger impacts from fast-growing and nitrogen-fixing range shifters.

Biotic characteristics

As with introductions, biotic characteristics of shifting species and recipient communities influence potential impacts (Fig. 1). Traits that make introduced species successful (for example, high fecundity, fast growth, generalist feeding habits, ability to engineer ecosystem conditions, and so on) will also facilitate the spread of range shifters (Hoving et al. 2013, Ramos JE, Pecl GT, Moltchanivskyj NA, Strugnell JM, León RI 2014, Ramos et al. 2015, 2018, Sunday et al. 2015, Estrada et al. 2016). Yet, because of the differences in shared evolutionary history with species in the recipient community, impacts on the recipient community are likely to differ (Fridley and Sax 2014b). Introduced species often benefit from interacting with new species (naïve prey, Cox and Lima 2006) and leaving old enemies behind (enemy release, Keane and Crawley 2002). In contrast, species undergoing climate-induced range shifts settle in an adjacent community, which is likely to have some overlap of species composition and interactions with the donor community (Sorte et al. 2010, HilleRisLambers et al. 2013). Such overlaps make it less likely that range shifters will leave enemies behind or encounter naïve prey, reducing the likelihood of novel impacts.

Yet there is evidence that range-shifting species can also experience enemy release (Engelkes et al. 2008, Katz and Ibáñez 2016), especially when a range shift occurs over a long distance or crosses a biogeographic boundary that previously limited dispersal (Frainer et al. 2017). The probability that a range shifter will experience release from natural enemies and encounter naïve species in the recipient community is higher at ecotone edges, where dissimilar adjacent communities meet (King et al. 2013). For example, the movement of tropical fish species to temperate communities has been facilitated by 'naïve' temperate algae with weaker chemical defenses. In the southeastern Mediterranean Sea, the expansion of tropical herbivores

led to a 60% loss in benthic biomass, a 40% decrease in species richness and, ultimately, a shift from a temperate reef system to one that more closely resembles adjacent tropical communities (Vergés et al. 2014). Such tropicalization of marine systems has become widespread as a result of range shifts (Wernberg et al. 2016, Vergés et al. 2016).

By applying an invasive ecology framework, we hypothesize that range shifters will be less likely to impact communities if some species have co-existed and interacted within the donor community. As with introduced species, the strongest impacts will likely be seen in recipient communities with high concentrations of specialist species (Clavel et al. 2011), populations with low genetic variability (Hoegh-Guldberg and others 2008), species that are already threatened by exploitation (Gurevitch and Padilla 2004) or species with low population sizes (Gurevitch and Padilla 2004). Communities with traits that confer high biotic resistance, such as high rates of predation, herbivory or strong competitive interactions (Levine et al. 2004), will be most resistant to impacts of range shifters (Sakai et al. 2001, Fig. 1).

Impacts of range shifting can parallel introductions

In contrast to introduced species, research on the effects of known range shifters has been relatively scarce despite several studies showing that the ecological and economic impacts can be equivalent (Carey et al. 2012). In marine systems, for example, range-shifting and introduced species can cause community-level effects of the same direction and magnitude, but these impacts have been studied in fewer than 10% of documented marine range shifts (Sorte et al. 2010). Here, we present several examples that illustrate how impacts of range shifters could have been predicted by applying an invasive species risk assessment framework based on the traits and associated impacts reviewed above.

Range shifters benefit from novel interactions

Range shifters encountering new species can have significant impacts on recipient communities through changes to biotic processes, such as predation, competition and the transmission of new parasites or pathogens. In North American forests, the southern flying squirrel (*Glaucomys sabrinus*) is displacing the smaller northern flying squirrel (*Glaucomys volans*) as the southern species expands its range in response to increasing temperatures (Wood et al. 2016). In addition to being superior competitors, southern flying squirrels are carriers of an intestinal parasite that is deadly to northern flying squirrels (Garroway et al. 2010, Krichbaum et al. 2010). In the same forests, white-tailed deer and their associated parasites are expanding northward in response to climate change (Kennedy-Slaney et al. 2018). Due to the introduction of these parasites as well as increasing thermal stress, moose, boreal specialists, are ultimately predicted to be extirpated from sites along their southern range edge (Weiskopf et al. 2019). Conversely, moose are expanding at the northern end of their range in response to the encroachment of deciduous forest into the tundra, leading to a decline in native caribou populations (Tape et al. 2016, Fig. 2). In addition to highlighting the complexity of the impacts of climate change, these examples show how some range shifters will cause localized extirpations, similar to introduced species. Risk assessments can be used to identify range-shifting pathogen carriers and communities with vulnerable species or naïve prey before such impacts occur.

Invasive traits in range-shifting species

As with introduced species that become invasive, range shifters with certain traits are more likely to have negative impacts. For example, many shifting tree populations are composed

of conifers, which often have biological traits that make them good colonizers. Most notably, many pine species have relatively high growth rates, are resistant to environmental stresses and develop monospecific stands that provide high propagule pressure (Richardson 1998).

Many invasive species that become dominant are also generalists, able to utilize a variety of different resources. In marine systems, ocean warming has allowed the long-spined sea urchin *Centrostephanus rodgersii*, previously limited by juvenile growth, to redistribute poleward from mainland Australia to Tasmania (Ling et al. 2009). This urchin consumes a wide range of macroalgal species, leading to significant declines in kelp forest habitat (Ling et al. 2015). Additionally, the long-spined urchin, a generalist herbivore, consumes many of the same prey species as the blacklip abalone (*Haliotis rubra*), a specialist. Reduction in resource availability has led to decreased abundance, fitness and survival among abalone populations (Strain and Johnson 2009). As with introduced species, range shifters that are generalist consumers and possess ‘weedy’ traits are more likely to impact a recipient community.

Community changes by range shifters can scale up to alter ecosystems

The abundance, role and trophic level of a species in its donor community can be indicative of its success in a recipient community (Bonebrake et al. 2018, Bradley et al. 2019). These effects on populations and communities can ultimately scale up to alter ecosystem states and processes. Ecosystem alterations can be observed as trees shift into new areas, leading to increases in aboveground and belowground biomass and shifts in nutrient cycling through litter decomposition (Wagg et al. 2014, Greenwood and Jump 2014, Lenoir and Svenning 2015, Lipton et al. 2018). Climate-related shifts of tree lines have been described in many parts of the world, and grasses are expanding in the tropics as fire frequency increases (Angelo and Daehler

2013). Yet the ecosystem impacts of these changes have been less explored than those that occur after invasions by introduced trees and grasses. Community and ecosystem effects have been observed in aquatic and marine systems as well. For example, herbivory by the long-spined sea urchin *C. rodgersii* has resulted in the collapse of kelp forests, leading to decreased biodiversity, a simplified food web and—at the ecosystem level—lower primary productivity (Filbee-Dexter 2014).

Another ecosystem shift occurring in tropical and subtropical regions is via the poleward expansion of mangroves into salt marshes (Demopoulos and Smith 2010). In Florida, mangrove forests have doubled their area at the northern end of their historical range due to reduced frequency of cold-weather extremes (Osland et al. 2013). Both mangrove trees and salt marsh grasses are foundation species in their respective ecosystems and play an important role in structuring communities by providing habitat and altering nutrient cycling (Osland et al. 2013). Because mangroves have greater aboveground biomass and, therefore, structural complexity than native salt marsh vegetation, their expansion has broad implications for coastal wetland ecosystems. The establishment of introduced mangroves in sandflats has increased the concentration of fine sediments and organic matter, leading to a higher abundance and diversity of non-native macrofauna (Demopoulos and Smith 2010).

The lack of defenses of temperate species to tropical herbivores (Bolser and Hay 1996, Burkepile and Hay 2008), general patterns of increased nutrient content with latitude⁸³ and increased disease due to increased herbivory (Silliman et al. 2013, Campbell et al. 2014) might accelerate the tropicalization of these temperate wetland regions under future climate change. Previous research on the impacts of biological invasions on ecosystem properties and processes has shown that these impacts are highly context-dependent, as the magnitude and direction can

vary both within and between types of impacts depending on taxa and ecosystems (Vilà et al. 2011). As with introductions, species that can alter the physical properties of the community (for example, ecosystem engineers) are most likely to have ecosystem-level impacts.

Balancing conservation with risk

Conservation options for promoting persistence (and preventing extinction) of species threatened by climate change include increasing habitat connectivity between communities to facilitate species movement and actively moving species—that is, assisted migration (McLachlan et al. 2007, Bonebrake et al. 2018). In the context of assisted migration to facilitate climate change adaptation, conservation organizations, such as the International Union for the Conservation of Nature (IUCN), are already considering invasion risk (Hawkins et al. 2015). However, increasing habitat connectivity to facilitate the movement of range-shifting species is generally considered an unmitigated good with little consideration of the full range of impacts on the recipient community.

Rather than placing a value on all species movements, we suggest using a risk–benefit analysis framework to assess potential impacts on a case-by-case basis. In some contexts, increasing habitat connectivity might best be based on analyses of donor and recipient communities with a focus on providing connectivity for low risk, nearby natives (Fig. 1). While there are inherent value judgements in assigning worth to species, we suggest that management should generally (1) facilitate range shifts that promote ecosystem services and biodiversity (Scheffers and Pecl 2019) and (2) discourage range shifts of species with the potential to negatively impact sensitive or rare species and communities (Stein et al. 2013). In some cases, the analyses will be straightforward. For example, when range-shifting species are both locally

and regionally uncommon, they could pose little risk to recipient communities (Fig. 1) and would benefit from opportunities to shift their ranges. This is unlikely to be true for species that have large impacts on their donor communities. Keystone predators (species with a disproportionate impact relative to their abundance) and foundation species (species that facilitate diversity by providing habitat and modifying their environment) might lead to management conundrums, as such species could pose great risk to recipient communities but also support the colonization of other range-shifting species with which they interact (Kreyling et al. 2011).

Even range-shifting species with small impacts in their donor communities can have large impacts in recipient communities because of ecological surprises, such as novel interactions with species in the community (Filbee-Dexter et al. 2017). A single invasion can be devastating to a community (Pimentel et al. 2005), and risk assessments are a useful and often-applied tool for identifying species of concern. Therefore, like others who warn about the potential dangers of assisted migration (Richardson et al. 2009), we propose that, before facilitating range shifts, the ecological, economic and societal impacts associated with these management actions be considered (Scheffers and Pecl 2019).

There are many assessment tools to evaluate the potential impacts of introduced species (Vilà et al. 2019). Notably, the Environmental Impact Classification for Alien Taxa (EICAT) framework is a standardized, objective and transparent approach adopted by the IUCN in 2016 that identifies the mechanisms through which introduced taxa can impact recipient communities (Blackburn et al. 2014, Hawkins et al. 2015). Although this assessment was developed for introduced species, the mechanisms of impact outlined in EICAT apply to the interactions between range shifters and recipient communities as well. Identified mechanisms primarily fall into the biotic characteristics of the Catford et al. (2009) framework and consist of competition,

herbivory and predation (including parasites and pathogens), hybridization, poisoning/toxicity, biofouling, ability to alter the ecosystem and interactions with other non-native species. These mechanisms are scored based on their magnitude of impact to the community, ranging from minimal (that is, negligible impacts, but no reductions in fitness for native species) to massive (that is, irreversible impacts through local, population or global extinctions; Fig. 3).

We suggest applying EICAT to rank and prioritize range-shifting species based on their potential impacts on recipient communities and to develop monitoring or control plans to limit those impacts. For example, communities receiving range-shifting species with the lowest potential to experience impacts (minimal and minor) are likely to benefit most from passive management actions, such as monitoring. Such range shifts could maintain or even increase community diversity and allow for persistence of populations under increasingly stressful environmental conditions. Although minor and moderate impacts lead to reductions of fitness in individuals or declines in population abundances, respectively, the recipient community structure and functioning are preserved. Future communities might not be analogous to existing recipient communities, but shifts are likely to have a net positive impact on global biodiversity.

Species with major or massive impacts, however, might need to be actively managed through facilitating or restricting movement, as their impacts could alter community structure and composition and cause local extinctions in the recipient community. While such changes, by definition within the EICAT framework, are reversible for species with major impacts, those with massive impacts are likely to cause irreversible changes as the community passes a threshold from which it can no longer recover. In the cases of species with major or massive impacts, serious consideration should be given to whether the benefits of promoting the persistence of the range-shifting species or populations justify the impacts on the recipient

communities. Based on approaches traditionally used to manage invasive species, we suggest the following specific strategies for range shifters:

- **Involve stakeholders early:** work closely with natural resource managers, conservation practitioners and decision-makers at every step of the process, including to identify priority ecological and cultural species (Garibaldi and Turner 2004, Enquist et al. 2017) and important ecological services (Pecl et al. 2017) associated with both range shifters and recipient communities.
- **Identify management priorities for range-shifting species and recipient communities:** what is the conservation status of the species? How important is the range shift for its persistence? How unique is the recipient ecosystem? How important are its constituent species and associated services for stakeholders? Supporting range shifts for species of conservation concern will remain a key climate change adaptation tactic for conservation practitioners and natural resource managers.
- **Incorporate species distribution model forecasts:** use the best available data and models to anticipate the movement of range shifters and identify high priority conservation areas, hotspots of biodiversity (Myers et al. 2000) and hotspots of high impacts (Ibáñez et al. 2009, Allen and Bradley 2016). Additionally, triaging which species are most likely to persist under projected climatic conditions can inform where resources can be most effectively allocated. Regularly revise management proposals to incorporate updates to these forecasts.
- **Use tools to assess invasion risk:** consider the parallels between traits common in successful introduced invasives (Pyšek and Richardson 2008, Fig. 1) and their potential

impacts (Blackburn et al. 2014, EICAT) to identify high- and low-risk range-shifting species.

- **Monitor changes in recipient communities:** monitor for shifts in abundance of target species and the arrival of new species, especially following disturbance and extreme climatic events (Colautti et al. 2006).

Challenges and potential limitations

Important knowledge gaps related to range-shifting species must be addressed to better understand the impacts that these species might have while also promoting persistence of species as their climate zones move. While range shifts have been documented for hundreds of species across taxa and ecosystems (Sorte et al. 2010, Chen et al. 2011, Pecl and Et Al 2017), they can be difficult to detect, as the historical ranges for many species are unknown or imprecise and our understanding of a ‘native range’ is not well-defined (Pereyra 2020). This is especially true for systems that are not as well-studied, such as deep-water marine systems that are difficult to access, and incorporating different spatial or temporal scales could further alter our definition of what constitutes a range-shifting species.

The impacts of range shifters, which might accrue more slowly than impacts of introduced species, have received less attention than invasion impacts; thus, our ability to predict future outcomes is limited. Range-shifting species could potentially undergo hybridization, experience toxicity, or evolve or adapt; an increased understanding of potential interactions in new environments is needed to evaluate these possible outcomes. Additionally, effects may differ across scales. Addressing these knowledge gaps will require working across broad

stakeholder groups to leverage and continue existing monitoring programs and incorporate diverse resources, such as local and traditional ecological knowledge (Raymond et al. 2010).

Predicting potential shifts is further complicated by our limited understanding of the abiotic and biotic limits to species' ranges. Predicting which species are likely to undergo shifts requires a knowledge of organismal physiology and thermal limits and how these contribute to ability to disperse as well as to adapt in place. Additionally, while temperature is a primary driver of distribution patterns (Hutchins 1947, Araújo and Pearson 2005), biotic resistance also plays a critical role (HilleRisLambers et al. 2013). Yet biotic interactions are, themselves, often altered by abiotic conditions (Zarnetske et al. 2012, Wallingford and Sorte 2019). Traits can act synergistically (for example, a drought causes reduced propagules), creating feedbacks that alter the magnitude of impacts. To detect species interactions and community impacts, manipulative in situ experiments are likely a necessary and important focus for climate change researchers. However, these experiments can be time-consuming or expensive, and a lack of experimental studies does not preclude using general risk assessment frameworks (Fig. 1) and knowledge from invasion biology to inform decision making. Additionally, risk assessments that are continually updated as new empirical data accrue can be used by practitioners, providing an accessible resource for those making management decisions.

Finally, we must acknowledge that anthropogenic climate change has led to unprecedented disruptions to global environments at a level rarely experienced before the Anthropocene (Barnosky et al. 2011, Blois et al. 2013). Many species' ranges have already been dramatically altered by human impacts, which raises questions about how to classify species that expand into their historical habitat following extirpation and which incarnation of a community should be protected (Wilmers and Getz 2005, Wilmers and Post 2006). The rapid rate of

anthropogenic climate change is likely to outpace species' ability to adapt. Range shifts, therefore, have been viewed as an alternative means to promoting global biodiversity. Yet, the potential feedbacks and consequences need to be considered as conservation goals may conflict with one another depending on the individual case. For example, mangroves and salt marshes provide similar ecosystem services. However, salt marsh systems have experienced significant area loss (Gedan et al. 2009), and range-shifting mangroves could further impact these vulnerable communities, highlighting the important of having clear objectives for management actions. At the same time, as range shifters are altering recipient communities, those communities themselves are responding to climate change; disentangling the causes and effects of these drivers will be a continuing challenge.

Conclusions

Although the impacts of range-shifting species can vary from minor to massive, considerations of species movements in the context of climate change has almost entirely focused on positive impacts (Hoegh-Guldberg and others 2008, Ricciardi and Simberloff 2009, Vilà et al. 2011). As species shift to track a changing climate, we have a unique opportunity to facilitate advantageous, and discourage potentially problematic, movement of species in real time. However, both researchers and managers will likely need to adopt a more fluid and dynamic view of what constitutes a community, as differences in species' responses could result in communities with no current analogue (Williams and Jackson 2007). Communities are unlikely to shift as a whole, and partial shifts will disrupt species interactions and lead to trophic mismatches (Tylianakis et al. 2010). Rather than developing new strategies to evaluate the potential impacts of range-shifting species, we suggest leveraging invasion ecology theory and

risk assessment tools (for example, EICAT) to quantify the magnitude of the potential impacts of range shifters and define specific conservation goals in response. This will allow us to maintain biodiversity and ecosystem functioning most effectively despite a rapidly changing climate.

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Table 1. Definitions of terms used in this manuscript.

Definitions	
Range shifter/range-shifting species	A species tracking its environmental niche through a range expansion or relocation beyond its historical native range.
Introduced species	A non-native species transported to a new ecosystem by humans, whether intentionally or unintentionally.
Invasive species	An introduced species that causes negative ecological, economic or environmental impacts.
Recipient community	The community into which an introduced or range-shifting species arrives.
Donor community	The community from which an introduced or range-shifting species originates.
Establishment	The process by which a founding population increases in size and becomes self-sustaining.
Spread	The process by which a species' range expands into new locations at an increasing distance from the original area of establishment.

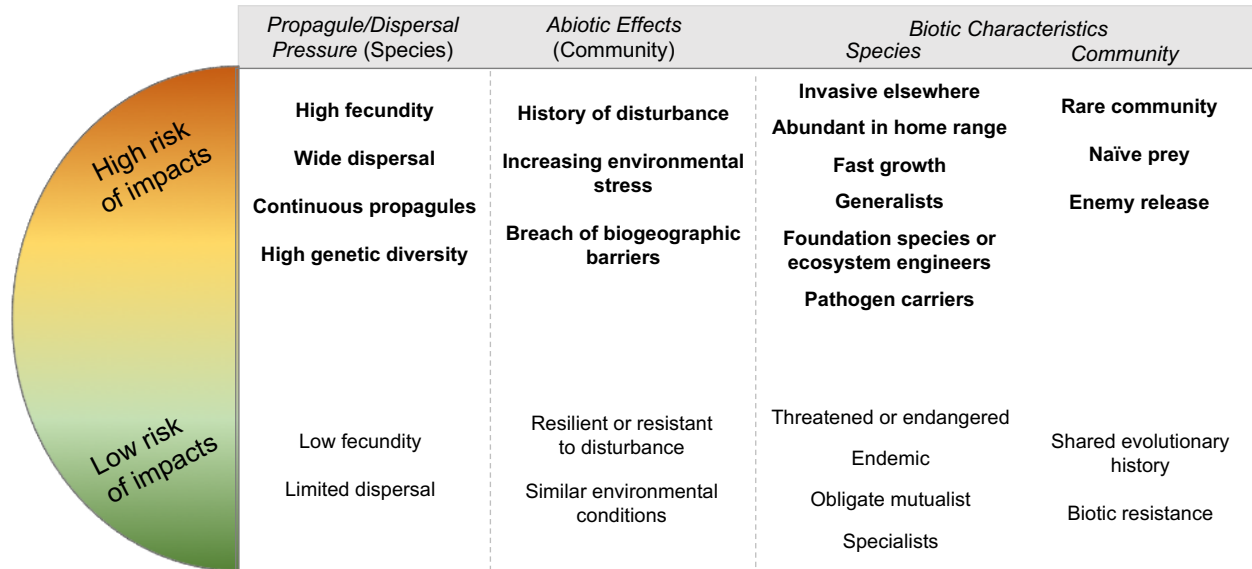


Fig. 1: Risk assessments for biological introductions focus on the importance of three main components that lead to the successful establishment and spread of species: the introduction of propagules, the abiotic environment and biotic interactions.

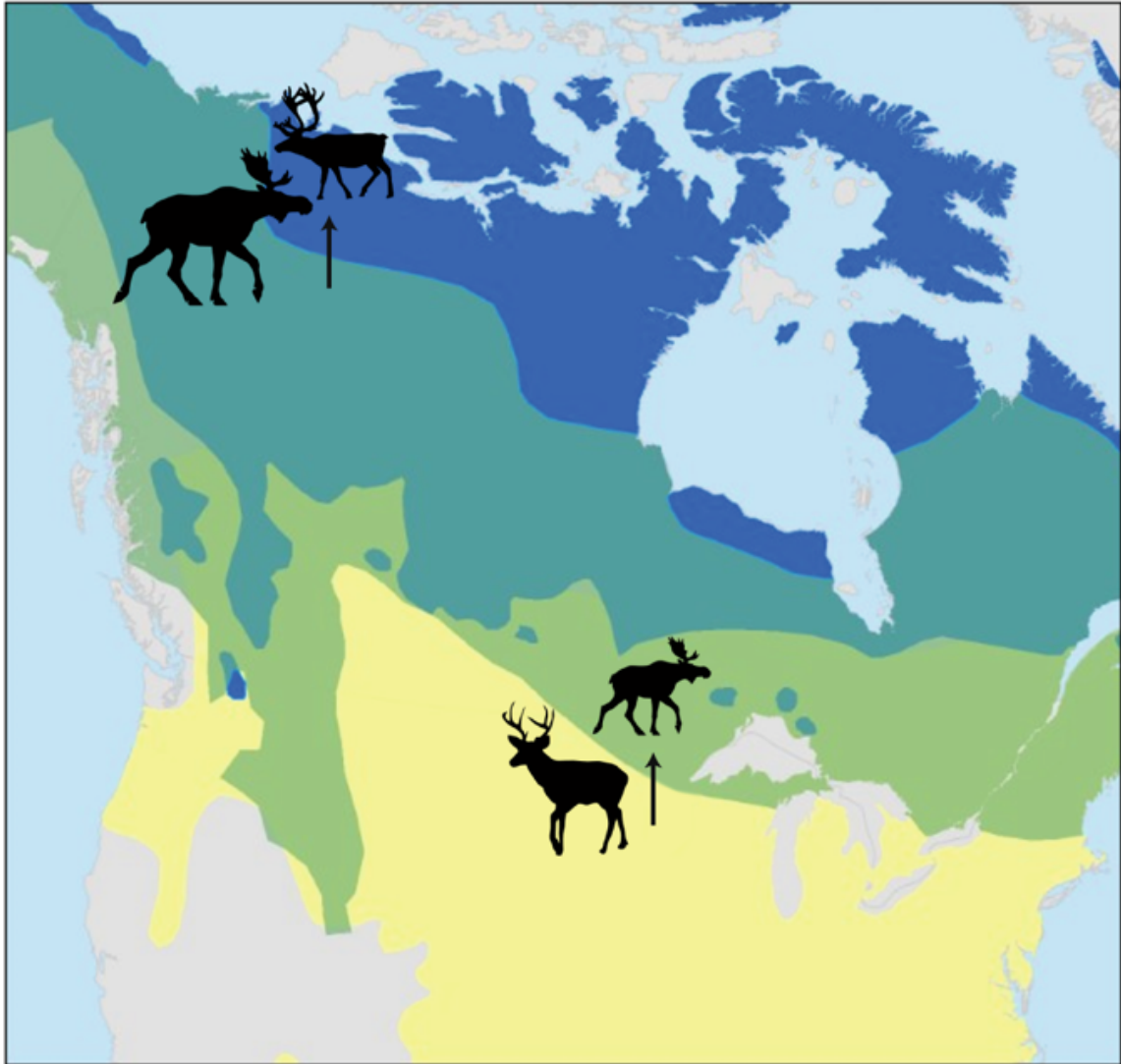


Fig. 2: Range shifters can impact recipient communities. For example, as white-tailed deer expand their range (yellow) northward (arrows pointing upwards) in response to climate change, moose at the southern edge of their range (green) are experiencing greater rates of parasitism and are projected to undergo population declines. In contrast, moose populations at the northern range edge are increasing and replacing caribou (blue). Smaller icons indicate range contractions. Ranges based on IUCN Red List of Threatened Species 2016.

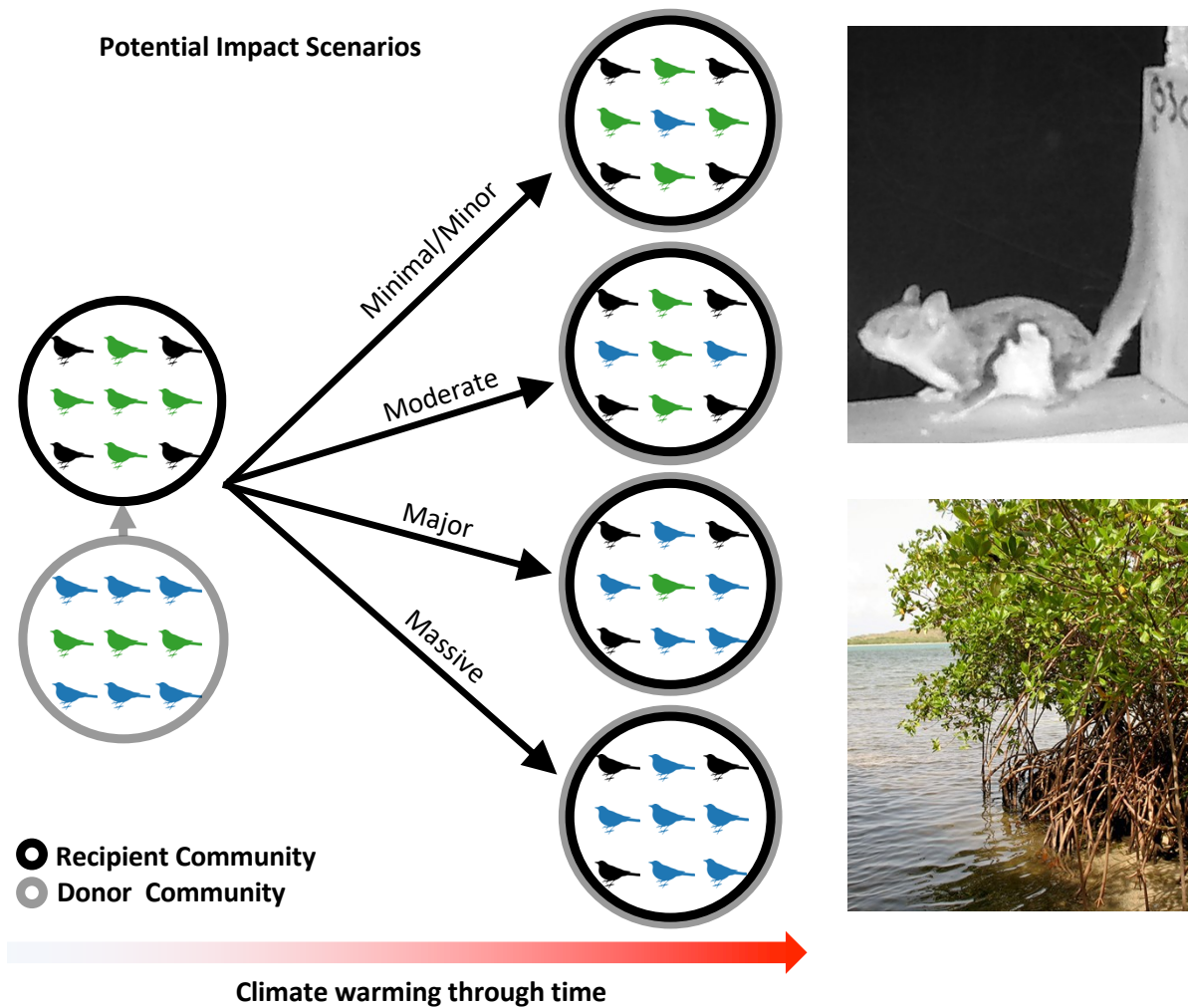


Fig. 3: As climate change alters environmental conditions, range shifts can lead to new species interactions and changes to community structures depending on the magnitude of associated impacts. For example, as individuals from a nearby donor community (blue birds in grey circle) shift into a novel recipient community (green and black birds in black circle) in response to climate change, they might have minimal or minor impacts (few blue birds in a community of primarily green and black birds) up to major or massive impacts where the shifting species predominates. This range of impacts can be seen in the examples discussed here, including cases of southern flying squirrels displacing northern flying squirrels (moderate due to effects on populations) to tropicalization (massive, irreversible shifts in ecosystems).

CHAPTER 3

Mexacanthina on the move: Range shifts of the dark unicorn whelk

Abstract

Across taxa and ecosystems, species are undergoing range shifts in response to climate change. However, the potential impacts of climate-driven range shifts on the communities they are moving into are not well understood. In southern California, the predatory whelk *Mexacanthina lugubris* has undergone a northward range expansion greater than 100 km over the past four decades. To assess the effects of *Mexacanthina* on local intertidal communities, we traced the history of the whelk's range shift and surveyed 10 southern California sites over the course of a year to determine spatial overlap with native whelk species (primarily *Acanthinucella spirata* and *Nucella emarginata*). Additionally, feeding experiments were conducted to assess strength of interactions with native whelks, and thermal tolerance trials were run to predict how future climate change could alter species' distributions and competitive abilities. We found that *Mexacanthina* was often more abundant than native species at sites where establishment had occurred. At the site level, spatial overlap of species depended on tidal elevation: *Mexacanthina* presence was associated with an increase in the occupancy and densities of native whelks overall, suggesting shared bottom-up drivers of prey and habitat availability, while this interaction between the presence and density of *Mexacanthina* and native whelks became negative at higher tidal elevations. In laboratory experiments, we found that the presence of *Mexacanthina* led to reduced growth in the native whelk *Acanthinucella* and that the range-shifting whelk was able to tolerate higher temperatures than the two common native species. While many, if not most, species are likely to undergo range shifts as a coping mechanism for changing climatic conditions, communities are unlikely to shift as a whole due to species-specific responses. By studying the impacts of range-shifting species, like *Mexacanthina*, we can better understand how climate change will alter existing community structure and composition.

Introduction

Climate change is altering populations and communities at an unprecedented scale, with the potential for irreversible losses of biodiversity (Bellard et al. 2012). As climate change continues and accelerates, many species are expected to become extinct, either locally or globally (Root et al. 2003, Thomas et al. 2004), and range shifts can limit these losses and protect global diversity. Range shifts, therefore, present an opportunity for persistence, as populations shift to more hospitable climates (Chen et al. 2011, Dawson et al. 2011). These climate-induced range shifts can occur at a variety of scales, including latitudinal shifts, as well as changes in elevation or depth (Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011), and have been reported across taxa and ecosystems (Parmesan 2006, Sorte et al. 2010, Poloczanska et al. 2013). For many species, range size can be the best predictor of extinction, with highly localized species at the greatest risk (Brooks et al. 2002, Sekercioglu et al. 2008). As a result, assisted migrations have become an important tool for conservation efforts aimed at protecting vulnerable or threatened species (Hoegh-Guldberg et al. 2007, Hodgson et al. 2009) or species that cannot acclimate or adapt to quickly changing climatic conditions (Berg et al. 2010). Nevertheless, there remains considerable debate within the scientific community regarding the costs and benefits of assisted migration (McLachlan et al. 2007, Wallingford et al. 2020)

The impacts of novel species in communities have been well-studied in the invasion literature, and range shifting species may similarly alter community dynamics. Range shifts vary greatly in rate and extent (Chen et al. 2011), and communities are unlikely to shift as a whole in response to climate change. Asynchronous and heterogeneous species responses can result in novel species interactions analogous to those seen in non-native species introductions and invasions (reviewed in Wallingford et al. 2020). However, few studies have assessed the effects

of range-shifting species (e.g. not directly introduced by anthropogenic activity) as they establish in new communities, despite the potential for significant impacts to communities and ecosystems (Sorte et al. 2010, Pecl et al. 2017, Wallingford et al. 2020).

Range-shifting species can consume, parasitize, or compete with native species that lack the ability or defenses to overcome them (Nackley et al. 2017). For example, a poleward range-shift of the long-spined sea urchin *Centrostephanus rodgersii* has led to declines in abundance, fitness, and survival of blacklip abalone (*Haliotis rubra*) due to increased resource competition (Strain and Johnson 2009, Ling et al. 2009). Similar to invasive species, impacts are likely to be greatest when the non-native species is abundant or occupies a high trophic level (Bradley et al. 2019). Furthermore, rare communities or those that have already experienced disturbance may be more susceptible to negative impacts (Dale et al. 2001). Endemic avian populations in Hawai'i, for example, have undergone population declines, reduced ranges, and extinction as a result of range expansions of the southern house mosquito, *Culex quinquefasciatus*, a vector for avian malaria (Fortini et al. 2015). Furthermore, range shifts can lead to trophic mismatches (Tylianakis et al. 2010) and result in novel communities with no current analogs (Williams and Jackson 2007). Understanding how communities will respond to range shifts is therefore an essential component of conservation and management practices aimed at protecting local and global biodiversity.

In coastal marine ecosystems, predatory mollusks can drive community structure (Lubchenco and Menge 1978, Hughes and Burrows 1993, Navarrete 1996), and the dark unicorn whelk, *Mexacanthina lugubris* (hereafter referred to by genus), appears to be shifting its range into southern California, USA. Native to Baja California, Mexico, its range was previously reported as extending from to Magdalena Bay, Baja California Sur (Marko and Vermeij 1999,

Fenberg et al. 2014). The whelk was first reported in large numbers in the San Diego area in 1974 (Radwin 1974), with significant expansion throughout San Diego by the 1990s (Hertz 1995), and has since expanded northward (Becker 2005). As of 2014, established *Mexacanthina* populations have been reported more than 100 km north of San Diego at Thousand Steps Beach in Laguna Beach, CA, USA (Fenberg et al. 2014). One individual was documented at a site more than 50 km away, and a shell was observed at a site 80 km away (iNaturalist.com, Table 1). Peak abundances also appear to be shifting northward. From 2002-2014, densities as high as 36 individuals per m² were found near Ensenada, Baja California, compared to only 2.4 per m² at Cabrillo National Monument (Fenberg 2014). It is unknown if *Mexacanthina* occurred in southern California prior to the 1970s: while there were no reports of live *Mexacanthina*, museum collections contain *Mexacanthina* shells that were collected in southern Orange County in 1937 and 1955 (Fenberg et al. 2014). The mechanisms of this recent expansion (or re-expansion) remain uncertain; like other whelks, *Mexacanthina* develop directly from egg sacs limiting the potential for dispersal via oceanic currents (Deng and Hazel 2010). Furthermore, rocky benches in southern California are often separated by significant expanses of sandy. However, it is possible that spread could occur via egg sacs attached to algae which can become wrack, individuals moving subtidally, or human transport whether intentional or accidental.

Mexacanthina could affect communities by altering existing species interactions, including by competing with native whelks. In southern California, whelks (Gastropoda) are important intermediate predators, and their relative impact may have increased following sea star declines due to wasting disease (Navarrete and Menge 1996, Cerny-Chipman et al. 2017). The most common native whelk species in southern California are *Acanthinucella spirata* and *Nucella emarginata*. Reported range limits for these whelks are Central California to Baja

California (Collins et al. 1996, Flagor and Bourdeau 2018), where they are found in low to mid intertidal zones, along with their primary prey, the California mussel *Mytilus californianus* and acorn barnacles *Chthamalus fissus/dali* and *Balanus glandula* (Connell 1970, Suchanek 1978, West 1986). Similar to native whelks in this area, *Mexacanthina* are reported to primarily feed on acorn barnacles (Marko and Vermeij 1999, Jarrett 2009), and they potentially consume mussels as well (Becker 2005).

Ecologically and taxonomically similar species are the most likely to interact strongly (Burns and Strauss 2011), and competitive exclusion can be an important driver of range limits and community composition on broad spatial scales (Case et al. 2005). However, changing environmental conditions can lead to a breakdown of historic biotic barriers (Van Der Putten et al. 2010). If native whelks and *Mexacanthina* are direct competitors, native whelks may be at a disadvantage: *Mexacanthina* are typically larger and more robust than native whelks, which could make them better at foraging or less susceptible to predation by crushing or gape-limited predators (Hughes and Elner 1979, Thomas and Himmelman 1988). Additionally, *Mexacanthina* have a larger foot per surface area, which is beneficial for avoiding forceful removal by predators or waves (Rilov et al. 2004, Guerra-Varela et al. 2009). *Mexacanthina* are also likely to be better adapted to heat and desiccation stress than native whelks due to their evolution in warmer and cooler locations, respectively.

We reviewed recent *Mexacanthina* sightings and conducted field observations and laboratory competition experiments to assess the impacts of *Mexacanthina* on southern California intertidal communities. Our study addresses the following specific questions: (1) is *Mexacanthina* continuing to expand northward?, (2) what are the potential impacts of

Mexacanthina on native whelks?, and (3) how might climate warming affect both local and range shifting whelks?.

Methods

To answer these questions, we reviewed historical and modern reports of *Mexacanthina* sightings and surveyed 20 intertidal sites for presence/absence of both native and range-shifting whelks to determine current distributions. At 10 of these sites, we also surveyed distributions and abundances of native whelks to assess whether the presence (and/or density) of *Mexacanthina* is associated with altered abundances and distributions of native whelks. Potential impacts were also assessed through a feeding experiment, in which we manipulated densities of predators and species composition of both predators and prey. Finally, to predict how climate warming could affect local and range shifting whelks, we conducted thermotolerance trials to assess each species' lethal temperature limits.

Abundance and Distribution

Evidence for *Mexacanthina* range shifts was collected from literature reviews, reports from biodiversity surveys conducted by the Multi Agency Rocky Intertidal Network (MARINE) and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), and community science data (iNaturalist, communication with authors). Based on reports of *Mexacanthina* sightings, we conducted presence/absence surveys at 20 sites in southern California, USA and abundance surveys across tidal elevations at 10 sites. Surveys were conducted quarterly beginning Fall 2017 through Summer 2018. Presence or absence of native whelks and *Mexacanthina* were determined using a 30-min timed count. During abundance surveys, we first

laid a 25-m horizontal transect along the waterline and then laid five transects perpendicular to the horizontal transect every 5 m (starting at the 5-m mark). Vertical transects extended from the waterline to bare rock. Along each transect, 1-m wide belts were surveyed, and the location of each whelk was recorded along the transect.

We used a Wilcoxon rank-sum test to compare average site densities (total whelks/area surveyed) of native whelks across sites with and without *Mexacanthina* and a Pearson's Chi-square test to compare intertidal distributions (average densities/tidal elevation) of *Mexacanthina* and native whelks. To evaluate the effects of *Mexacanthina* (both presence and density) and tidal elevation on native whelks (presence and density), densities for each tide height (number of individuals/area in m²) were calculated from belt transect data for bins encompassing 0.25-m in vertical tidal elevation. Data were zero-inflated and overdispersed; we averaged tide height densities across transects at each site and used gamma mixed-effects hurdle models, analyzing 1) data containing zero and non-zero values based on a binomial distribution and 2) non-zero data based on a gamma distribution. We examined the effects of tide height, *Mexacanthina* presence and density, and their interaction on native whelk presence and density; significance was evaluated via Wald Chi-square tests. Models were run using the lme4 package (Bates et al. 2015) in R (R Core Team 2015).

Species Interactions

To evaluate the potential for interactions between *Mexacanthina* and native whelks, we manipulated species composition and density in a laboratory experiment using *Mexacanthina* and the most common native whelk *Acanthinucella* (referred to as M and A in treatments). Whelks of both species were collected from Treasure Island Beach, where both species are

abundant, in Laguna Beach, CA (Fig. 2). Individuals of similar sizes were collected to minimize differences in metabolic demand. Four tanks with programmed tidal cycles were used to simulate natural conditions experienced by the whelks and prey species, with low tide occurring twice daily for 2-hrs and a 12-hr light period. Our experimental units were 11 x 11 cm mesocosms that contained 10 x 10 cm sandstone tiles. Whelks were exposed to three prey treatments: mussels only, barnacles only, or a mix of both prey species. Whelks (up to 2 individuals per replicate, as described below) were continuously provided adequate prey items so that resources were not limited (either 4 mussels or 4 barnacle-covered shells). Mussels (32.76 ± 4.47 mm length) with and without barnacles were collected from Little Corona Beach in Newport Beach, CA. In the barnacle treatments, we provided barnacles attached to mussel shells that had the soft tissue removed. The number of barnacles per shell was counted before the shell was attached to the tile using silicone. In the mussel treatments, mussels were scraped clean of epibionts and measured (l x w x h). Mussels were then also attached to the tiles using silicone to ensure uniformity in surface area and distance between prey.

To quantify the strength of interactions and density-dependent effects of the whelks, we used six predator treatments consisting of 1 individual of each species (A, M), 2 individuals of each species (AA, MM), 1 + 1 individual of each species (AM), and a control with no whelks (C; to account for any non-consumptive mortality across tanks). This was a randomized complete block design with 18 separate predator x prey treatments and a total of $n = 4$ replicates of each treatment (one per tidal tank, our blocking factor). Whelks were starved for one week prior to the experiment and were randomly assigned to treatments. Mussel mortality was assessed weekly, at which time mesocosm locations were shuffled within each tidal tank to minimize location

effects. Barnacle mortality was assessed visually after four weeks (to ensure there were live prey remaining) and was quantified at the conclusion of the eight-week experiment.

Measurements of whelk shell and aperture length and width, as well as buoyant wet weight (Palmer 1982), were collected at the start and end of the experiment; dry weight was also determined at the end of the experiment. To compare biomass consumed between prey treatments, we created regression curves for biomass (ash free dry weight) to dimensions (mussels, $R^2 = 0.89$; Appendix, SFig1. 1) and biomass to number (barnacles, $R^2 = 0.83$). Prey mortality in control tanks was not used in the analyses as no mussel mortality occurred within the control treatments, and average barnacle mortality across tanks was 2.25 ± 0.48 , accounting for less than <1% of total mortality. Two-way ANOVAs were used to assess the how prey (mussels, barnacles, or both) and predator composition (A, M, AA, MM, AM) affected biomass consumed and whelk growth (% change in mass), with initial whelk mass as a co-variate. Data were log-transformed to meet assumptions of normally distributed residuals. We did not include tank (our blocking factor) in the model as it accounted for less than 0.01% of the variance and did not significantly improve the model fit.

Thermal Tolerance

To determine the effects of temperature on each species, we estimated upper and lower lethal thermal limits for *Mexacanthina*, *Nucella*, and *Acanthinucella* by calculating each species' LT_{50} , or the temperature lethal to 50% of individuals. Whelks ($n = 5$ per species per temperature) were placed in 1.5 mL centrifuge tubes with a piece of seawater-soaked chamois cloth (to prevent desiccation). We then randomly assigned whelks to one of six temperature treatments: 0°C, 18.5°C (ambient temperature), 32°C, 35°C, 38°C, and 41°C. Using 28 L digital water baths,

tubes were heated from ambient to treatment temperatures over a 40 min period (Sorte et al. 2019). Following a 6-h thermal exposure, whelks were transferred to a recirculating seawater system for an 18-hr recovery period, at which time mortality was assessed. Logistic regressions were used to calculate LT_{50} , as well as differences in survival between species and treatments.

Results

Northward Expansion

During presence/absence surveys, *Mexacanthina* was found at 10 of the sites we surveyed (in 7 sites, it was found year-round), including 4 sites north of its previously documented range (Fig. 2). Native whelks were found year-round at 19 of the 20 sites that we surveyed). Across sites, average *Mexacanthina* densities (where present) ranged from between 0.05-4.27 individuals per m^2 (Fig. 2). During our surveys, we found the highest densities of *Mexacanthina* at Thousand Steps (maximum of 24.55 individuals per m^2). Average native whelk densities ranged from 0.14-0.84 individuals per m^2 .

Potential Impacts

Spatial overlap between *Mexacanthina* and native whelks was assessed at both the site level and across tidal elevations within a site. There was not a significant difference in native whelk densities between sites where *Mexacanthina* was present and sites where *Mexacanthina* was absent ($W = 136$, $p = 0.11$). However, there was a significant difference in the distribution of native whelks and *Mexacanthina* across tidal elevations. *Mexacanthina* was found at higher tidal elevations than native whelks ($\chi^2 = 63$, $p = 0.02$; Fig. 3).

A hurdle (two-step) model was used to evaluate the effects of *Mexacanthina* (presence and density) and tidal elevation on 1) native whelk presence and 2) density. We found a positive association between *Mexacanthina* and native whelk presence, which was driven by spatial overlap at low elevations, whereas native whelks occurred less often at high elevations with *Mexacanthina*. Regressions (binomial distributions) showed that the probability of native whelks being present increased significantly when *Mexacanthina* was present ($\chi^2 = 19.36$, $p < 0.001$; Table S1, Fig. 4) and as *Mexacanthina* density increased ($\chi^2 = 17.78$, $p < 0.001$). *Mexacanthina* was found at higher tidal elevations within the intertidal than native whelks (Fig. 3) while native whelks were found less often as tidal elevation increased ($\chi^2 = 10.85$, $p < 0.001$; $\chi^2 = 16.36$, $p < 0.001$). Native whelk presence was also impacted by the interactions between tidal elevation and *Mexacanthina* ($\chi^2 = 10.69$, $p = 0.001$; $\chi^2 = 14.47$, $p < 0.001$): native whelk occurrences increased with *Mexacanthina* at lower tide heights whereas they were less likely to occur at higher tidal elevations when *Mexacanthina* was present and at high abundance.

When present, native whelk densities showed a similar pattern as described above for native whelk occupancy: there was a positive association between native whelks and *Mexacanthina* at low elevations, and a negative association at high elevations. Native whelk densities did not change with *Mexacanthina* presence ($\chi^2 = 1.43$, $p = 0.23$), and tidal elevation had no main effect on native whelk densities ($\chi^2 = 0.03$, $p = 0.86$; $\chi^2 = 0.35$, $p = 0.55$). However, native whelk density tended to increase with increased *Mexacanthina* density ($\chi^2 = 3.45$, $p = 0.06$), and there was a significant interaction between tidal elevation and *Mexacanthina*. Native whelk densities decreased at higher tidal elevations when *Mexacanthina* was present ($\chi^2 = 7.79$, $p = 0.005$) and as *Mexacanthina* densities increased ($\chi^2 = 5.67$, $p = 0.02$).

In the competition experiment, biomass of prey consumed differed across prey treatments ($F = 3.99$, $p = 0.03$, Table S2), but there was no effect of predator treatment ($F = 1.80$, $p = 0.15$) or the interaction ($F = 0.38$, $p = 0.92$; Fig. 5). Both *Mexacanthina* and native *Acanthinucella* consumed more biomass in treatments containing only mussels compared to those containing only barnacles (Fig. 4). Whelk growth (% change in mass) did not differ across prey treatments ($F = 0.71$, $p = 0.52$), but there was a significant difference between predator treatments ($F = 6.38$, $p < 0.001$), with the presence of *Mexacanthina* leading to slower growth of *Acanthinucella* (AM vs. A and AA treatments). There was not a significant interaction between xx and xx on xx ($F = 0.71$, $p = 0.71$).

Future Climate Warming

Thermotolerance assays resulted in LT_{50} values of 38.1°C for *Mexacanthina*, 36.5°C for *Acanthinucella*, and 32.1°C for *Nucella* (Table S3). There was a significant difference in survival between temperature treatments ($\chi^2 = 90.80$, $p < 0.001$; Fig. 6) and species ($\chi^2 = 27.45$, $p < 0.001$). A Tukey Post-hoc test showed that *Mexacanthina* and *Acanthinucella* had similar LT_{50} values ($z = 1.61$, $p = 0.22$), both of which were significantly higher than LT_{50} values of *Nucella* ($z = -2.99$, $p = 0.007$ and $z = -2.66$, $p = 0.02$, respectively).

Discussion

We found that *Mexacanthina* is continuing to expand northward and that the range-shifting whelk has the potential to alter the composition of the communities into which it is moving. The range-shifter utilizes analogous prey resources and rocky intertidal habitats as native whelk species, and at sites where both native and range-expanding whelks are present,

Mexacanthina densities are often an order of magnitude higher than densities of native species. Furthermore, *Mexacanthina* are able to utilize more space at higher elevations in the intertidal habitat, and at sites where *Mexacanthina* is present, native whelks occur in lower abundances at these higher tidal elevations. In a manipulative feeding experiment, the native whelk *Acanthinucella* grew less than *Mexacanthina* in treatments that contained *Mexacanthina*, regardless of prey type. Under future climate warming, *Mexacanthina* populations are likely to be at an advantage, and potentially increase, given that they have higher thermal tolerances and occupy warmer habitats than native whelks.

Over the course of a year, we were able to (by direct observation) definitively confirm the presence of *Mexacanthina* at 4 sites north of its previously documented range edge at Thousand Steps (TS), the farthest approximately 5 km away. However, we did not observe - and were therefore unable to confirm - the presence of *Mexacanthina* at other sites where it had been previously reported. Our surveys do not necessarily preclude the presence of *Mexacanthina* at these locations; reports of individuals at other sites indicate that dispersal could be ongoing, but low densities might preclude observation in our surveys. Additionally, because many of the reported sightings were from community scientists, there is limited information available about search effort. During our surveys, occurrences were spotty across seasons at Heisler Park, the furthest north site where we observed *Mexacanthina*. As populations at the range edge become well-established, increased and more consistent propagule pressure could lead to greater numbers of individuals at these more distant locations (Gaines et al. 2007). Furthermore, the methods through which *Mexacanthina* are moving to new sites remain unclear, which makes establishing range limits difficult.

As *Mexacanthina* shifts north, it has the potential to disrupt existing community dynamics through interactions with local species. *Mexacanthina* utilize similar habitats and resources as native whelks, which primarily prey on the California mussel *Mytilus californianus* and the acorn barnacles *Chthamalus dalli/fissus* and *Balanus glandula* (West 1986, Deng and Hazel 2010). Native whelks were more likely to be present at sites where *Mexacanthina* were present (and at higher densities). This is likely due to greater prey availability, specifically mussels, at these sites, representing a bottom-up effect acting on both native whelks and *Mexacanthina*. This is supported by the high abundances of native whelks at Shaw's Cove (SC) and Crystal Cove (CC), where prey levels are comparable to sites supporting both species. Although they share habitat space and prey resources, in most locations, prey is currently unlikely to be a limiting resource, which might limit competition. However, if prey species continue to decline (Smith et al. 2006), then the potential for competitive impacts could increase.

Despite the currently low probability of direct negative impacts via competition (due to high prey availability), our results do suggest that there could be negative trait-mediated impacts of *Mexacanthina* on native whelks. At sites with *Mexacanthina* and when *Mexacanthina* densities are high, native whelks were negatively associated with *Mexacanthina* at high tidal elevations. This may suggest that elevational distributions of natives have shifted downwards in the presence of an expanding species. For intertidal whelks, abiotic and biotic stress typically determine intertidal distributions with higher abiotic stress in the high intertidal compared to high biotic stress in the low intertidal (Menge and Sutherland 1976). Lower tidal elevations are associated with high levels of predation from subtidal species, which feed during high tide (Paine 1969, Rilov and Schiel 2006). Increased use of higher tidal elevations by *Mexacanthina* while native whelks primarily inhabit lower tidal elevations could potentially be explained as niche-

partitioning that could allow for co-existence between the expanding and native species. By utilizing areas lower in the intertidal, native whelk species could be minimizing physical stress, especially as *Mexacanthina* appear to be more heat tolerant than some native species.

Another potential mechanism that could explain the negative association between *Mexacanthina* and native whelks at higher tidal elevations is intraguild predation, in which predators consume species at their same trophic level with whom they share prey items. Previous studies have reported acorn barnacles as *Mexacanthina*' primary prey (Marko and Vermeij 1999, Jarrett 2009; although see Becker 2005). However, we found that the whelks consumed greater numbers of mussels in lab conditions and consumed a diverse set of prey items in the field, including herbivorous gastropods and other whelks. In addition to being consistent with our survey results (i.e., the negative association between native and expanding species at high elevations), intraguild predation could explain native whelks' reduced growth if *Acanthinucella* are less likely to forage when an intraguild predator is present (Holt and Polis 1997). Previous studies support the presence of trait-mediated effects of intraguild predators on native whelks: when sea stars are present, *Nucella* forage less often, experiencing reduced growth and reproductive ability (Gosnell et al. 2012), and even undergo shifts in diet (Sanford et al. 2003). While no predation between whelks occurred during lab experiments, future field experiments could help elucidate the relationship between the whelks, both as competitors and potential intraguild prey.

Understanding the interactions between biotic and biotic factors is increasingly important as future climate change could further limit native whelks' habitat. Temperatures in southern California coastal communities are expected to increase by 1.8 to 5.5°C in the coming century (Cayan et al. 2008). As temperatures increase, populations living at or near their thermal limits

will likely experience declines leading to range contractions (Wallingford and Sorte 2019, Sorte et al. 2019). Additionally, metabolic demands increase with warming, requiring greater amounts of time spent foraging to meet the same energetic demands and exposing whelks to greater risk from both biotic and abiotic factors (Sanford 2002). Because of its greater thermal tolerance, *Mexacanthina* could access more prey and habitats than native whelks and spend longer amounts of time at tidal elevations where the species overlap. Rising temperatures might result in downward range contractions for both species, whereby native whelks could experience both greater abiotic stress (at their upper elevation physiological limits), as well as greater predation risk (from subtidal predators).

Evidence for climate-driven range shifts often include a range contraction at the range edge that is becoming more physically stressful (Sheth and Angert 2018). Decreasing *Mexacanthina* populations in southern Baja California support this assessment. Museum collections indicate a shift in the southern range edge, previously reported to be Magdalena Bay, Baja California Sur. Surveys conducted in 2014 found no *Mexacanthina* in Baja California south of 26.05°N, while specimens were collected in 1950-1979 from areas between 23.9 and 24.8°N (Fenberg et al. 2014). The northward expansion of *Mexacanthina* may be due to increased environmental stress (and, thus, greater mortality and resources) experienced by local species at sites of expansion. Despite reported ranges extending into Baja California Sur, biodiversity surveys conducted in 2003, 2007, and 2011 found *Nucella* at only 2 of 12 sites (one in 2003 and one in 2007), with population densities less than 0.1 per m² and *Acanthinucella* was not reported at any Baja California sites (Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), The Multi-Agency Rocky Intertidal Network (MARINE)). Similarly, community science data

from iNaturalist shows only one report of *Acanthinucella* in Baja California (2019) and no reports of *Nucella*.

Interestingly, the native California whelk *Acanthinucella spirata* has also recently undergone a northern range shift in response to climate change (Hellberg et al. 2001, Flagor and Bourdeau 2018). This poleward range shift shares a number of similarities with that of *Mexacanthina*. Namely, new populations have been documented two degrees north of its previously documented range despite direct-developing young with limited dispersal (Flagor and Bourdeau 2018). Possible mechanisms for the expansion include avian-mediated dispersal (Green and Figuerola 2005) or rafting on kelps (Thiel and Gutow 2005), mechanisms which could account for the non-contiguous expansions seen in *Mexacanthina*.

While many, if not most, species are likely to undergo range shifts as a coping mechanism for changing climatic conditions, species specific responses could lead to community fragmentation if species shift asynchronously, as appears to be the case with the whelk guild presented here. While *Mexacanthina* and *Acanthinucella* both appear to be experiencing a northward climate-driven range shift, there are no reports of a similar range shift for *Nucella*. If endemic species become locally extinct, range-shifting species may be able to fill a comparable niche, but there are likely to be long-term effects, such as a shift in native predatory snail assemblages and changes to population dynamics of prey species (Flagor and Bourdeau 2018). Because communities are unlikely to shift as a whole, climate-driven range shifts therefore have the potential to alter community composition and ecosystem functioning through changes to species interactions. In some cases, range-shifting species will compete with natives that are not able to undergo range shifts (or are unable to shift on pace with climate change), potentially leading to local extinctions.

In this study, we found that the dark unicorn whelk *Mexacanthina lugubris* is undergoing a northern range expansion, with native whelks displaying altered distributions in the field when the expanding species is present and changes to energy allocation in the lab when the range-shifter is present. Furthermore, native whelks are likely to experience greater impacts as climate change continues and accelerates, due to greater vulnerability to abiotic stress. Although species composition of this intermediate predator guild is likely to change in the future, ecosystem functioning might be maintained through functional redundancy as *Mexacanthina* appear to fill a similar niche as *Acanthinucella* and *Nucella*. Future communities may be different than those we recognize today, but range shifts present an opportunity for individual species and ecosystem services to persist in the face of climate change.

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Tables and Figures

Table 1. Survey sites and reports of *Mexacanthina* presence. For sites where *Mexacanthina* has been reported north of its published limit of Thousand Steps Beach, Laguna Beach, California, USA (Fenberg et al. 2014), the date and source of the first report is given. Shaded sites represent locations of abundance and density surveys, in addition to the presence/absence surveys. Reported sightings are collated from published sources, monitoring projects, and citizen scientist observations. Sites are indicated as confirmed when *Mexacanthina* was found at least once during seasonal presence/absence surveys.

Site (N to S)	Latitude	Longitude	Reported	Confirmed
Leo Carillo Beach (MB)	34.044	-118.937	iNaturalist 2017 *	No
Point Fermin (PF)	33.705	-118.295	No	No
Fisherman's Cove (FC)	33.446	-118.485	Pers. Comm. 2017	No
Little Corona (LC)	33.588	-117.867	No	No
Crystal Cove (CC)	33.570	-117.837	No	No
Crescent Bay (CS)	33.547	-117.805	iNaturalist 2017	No
Shaw's Cove (SH)	33.544	-117.800	iNaturalist 2018	No
Heisler Park (HP)	33.543	-117.793	MARINe 2013	Yes
Victoria Beach (VB)	33.520	-117.765	iNaturalist 2019	Yes
Treasure Island (TI)	33.514	-117.761	iNaturalist 2017	Yes
Table Rock (TR)	33.502	-117.747	Pers. Comm. 2018	Yes
Thousand Steps (TS)	33.493	-117.739	Yes	Yes
Dana Point (DP)	33.460	-117.715	Yes	No
Carlsbad (CB)	33.132	-117.337	Yes	Yes
Swami's (SW)	33.035	-117.294	Yes	Yes
Cardiff (CR)	33.000	-117.279	Yes	Yes
Scripps (SC)	32.873	-117.253	Yes	Yes
Wind and Sea (WS)	32.830	-117.281	Yes	Yes
Sea Ridge (SR)	32.808	-117.267	Yes	Yes

* Empty *Mexacanthina lugubris* shell



Figure 1. Color morphs of the range-shifting dark unicorn whelk *Mexacanthina lugubris*.

Mexacanthina is distinguished from other intertidal whelks by its robust body, pronounced ridges and whorls, and the presence of a spine at the base of the aperture. Photographs by P.

Wallingford.

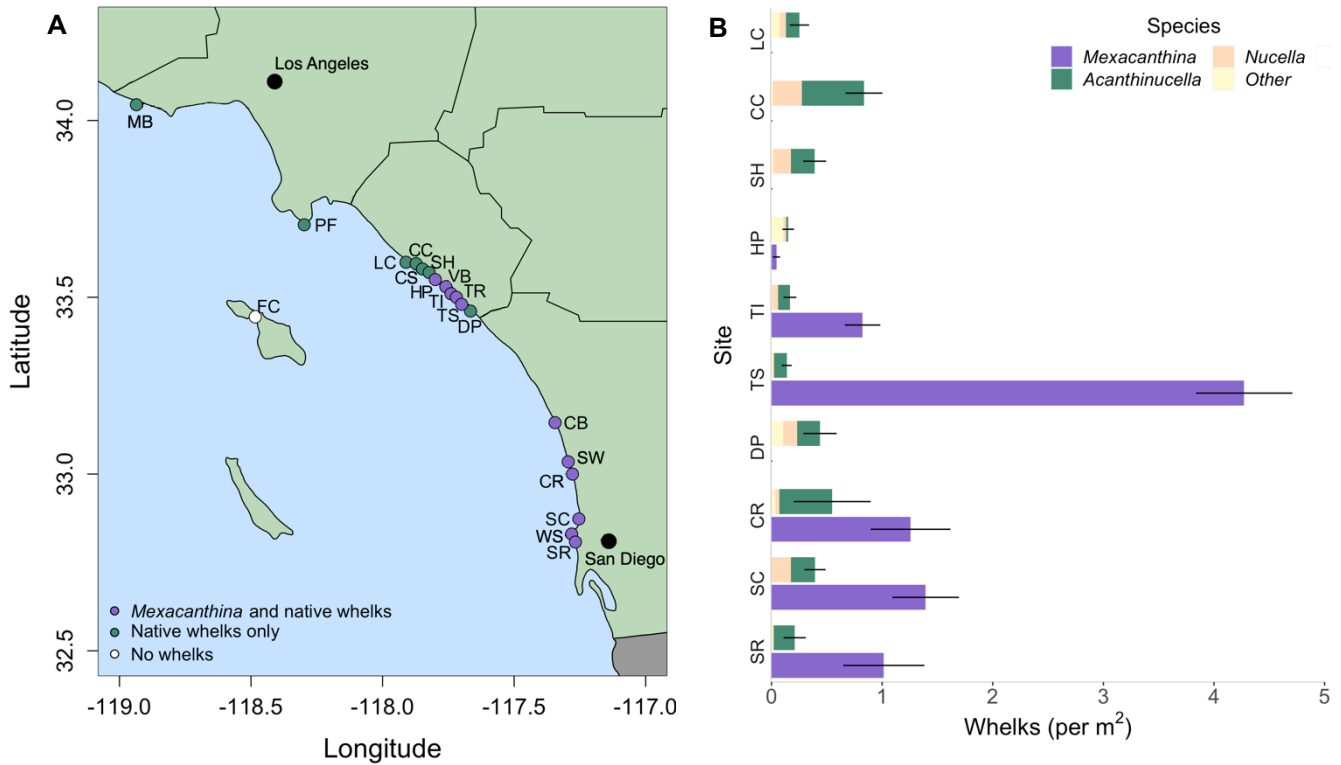


Figure 2. (a) *Mexacanthina* were found at 9 of 20 sites surveyed (Table 1), including four sites north of its previously published range limit at Thousand Steps Beach, Laguna Beach, CA (TS). Native whelks were found at 19 of 20 sites. (b) Average densities of common whelk species at 10 sites. Values are average densities across 5 transects and 4 seasons; error bars represent standard error (for *Mexacanthina* and the sum of all native whelks species) .

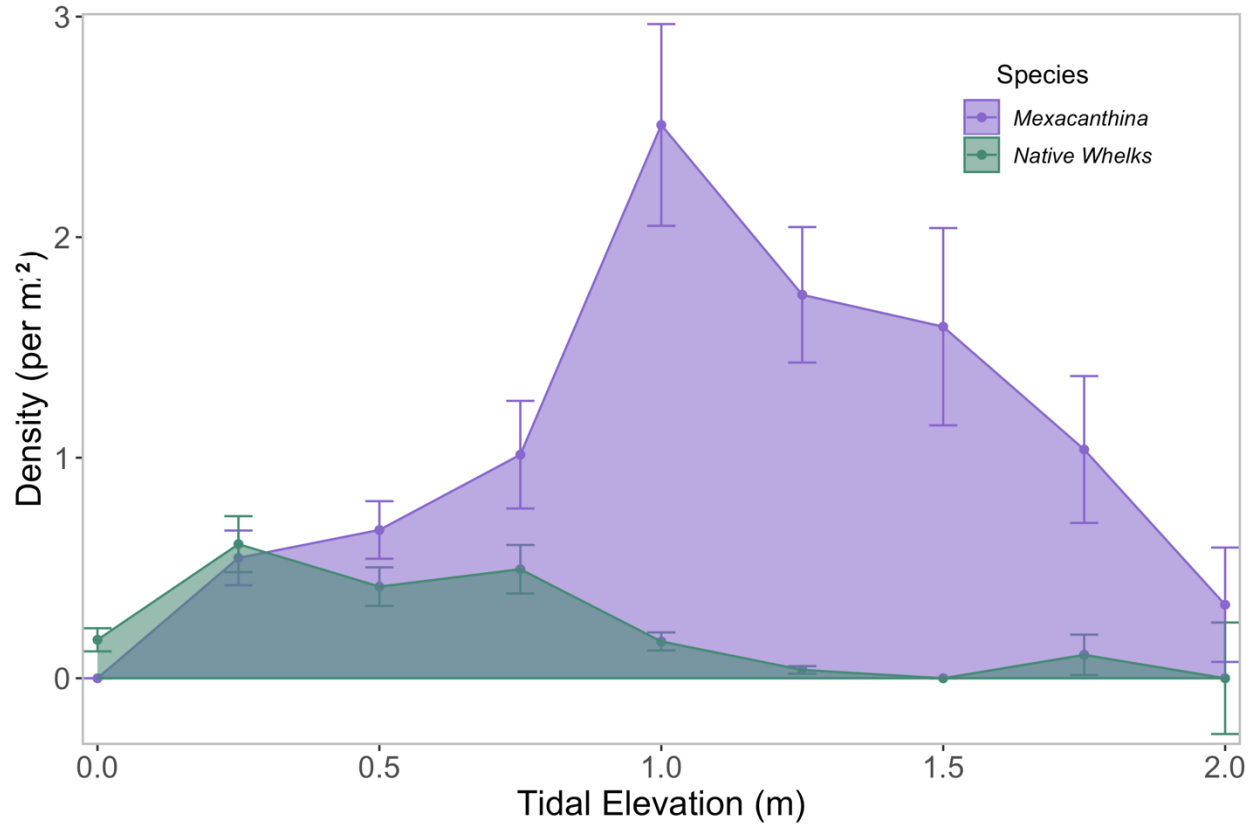


Figure 3. Average densities \pm SE of *Mexacanthina* and native whelks across tide heights. Native whelk densities peaked \sim 0.75m lower in the intertidal than those for *Mexacanthina*. Data Values are averaged across sites and seasons (n = 40).

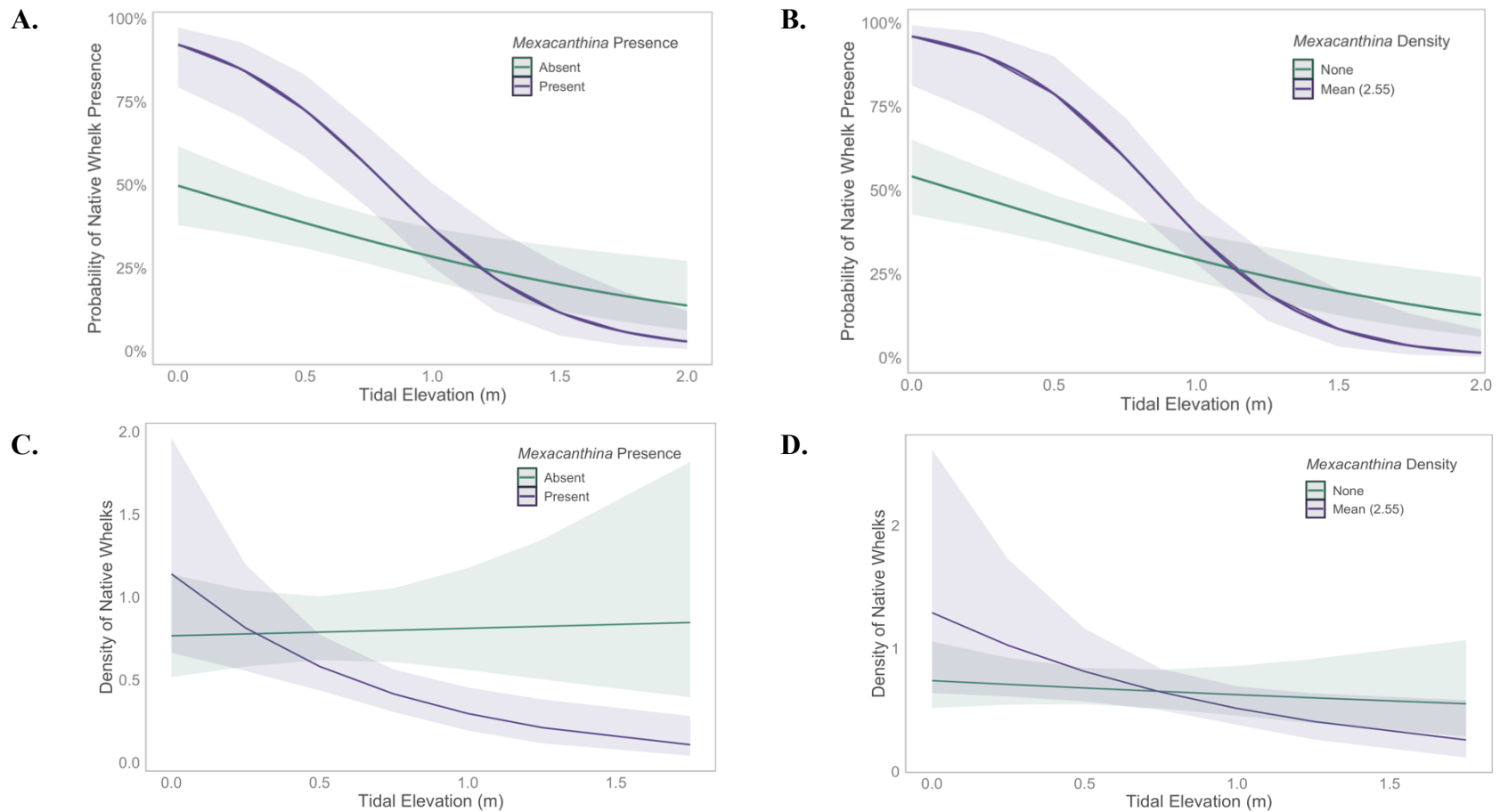


Figure 4. There was positive association between *Mexacanthina* and native whelk presence, which was driven by spatial overlap at low elevations, whereas native whelks occurred less often at higher elevations when *Mexacanthina* was A) Present and B) as *Mexacanthina* density increased (binomial distributions). Native whelk density (> 0) decreased significantly across tidal elevations with C) *Mexacanthina* presence and D) density (Gamma distributions). Figures show responses of native whelks across transects, sites, and seasons ($n = 200$) \pm SE.

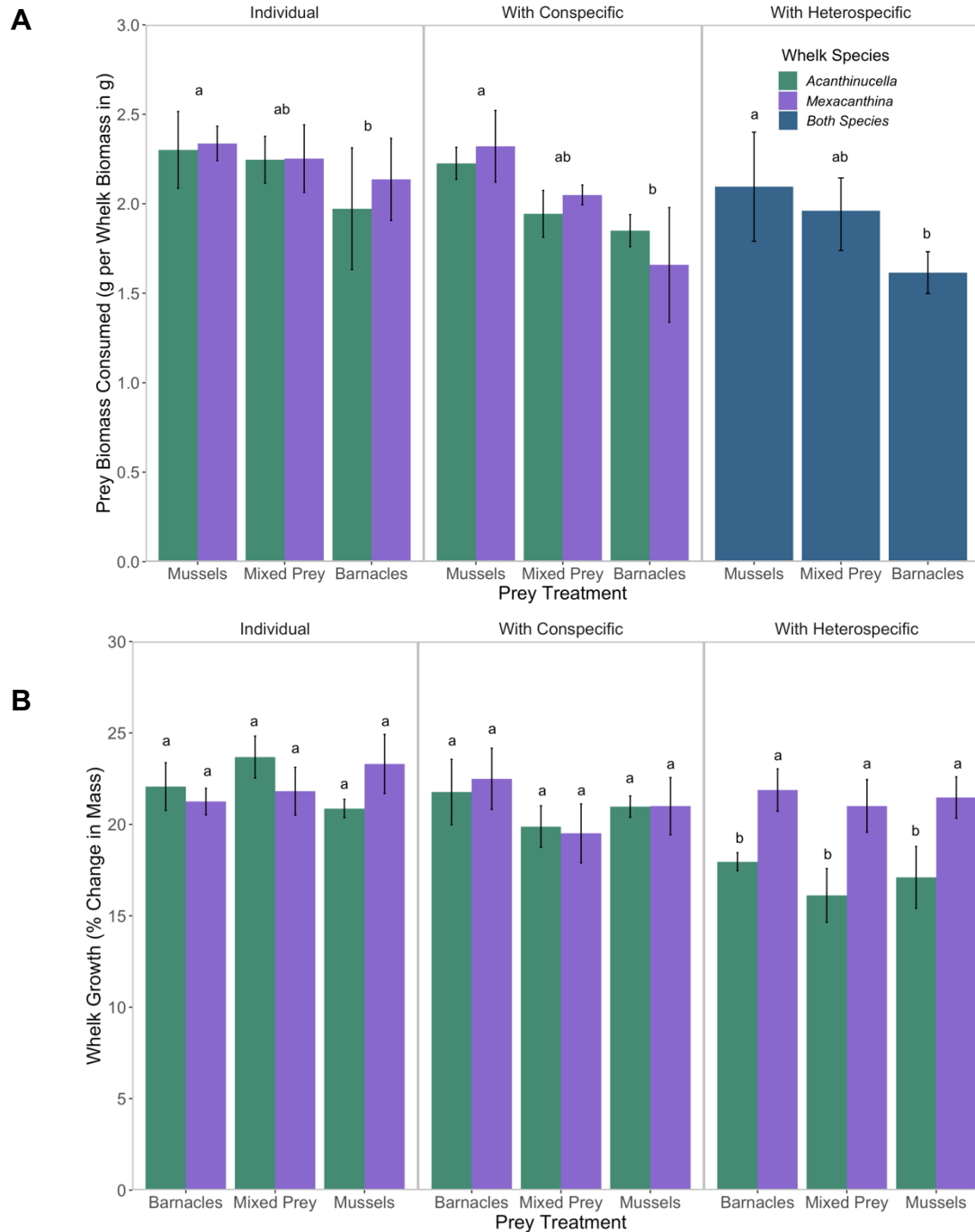


Figure 5. (a) Average biomass of prey consumed (g) per whelk biomass (g) varied across prey treatments, with less biomass consumed in barnacle only treatments compared to mussel only treatments during the course of the experiment. (b) Percent change in whelk mass over the course of the experiment. *Acanthinucella* experienced reduced growth in mixed-predator treatments. Values are averages of N = 4 replicates \pm SE.

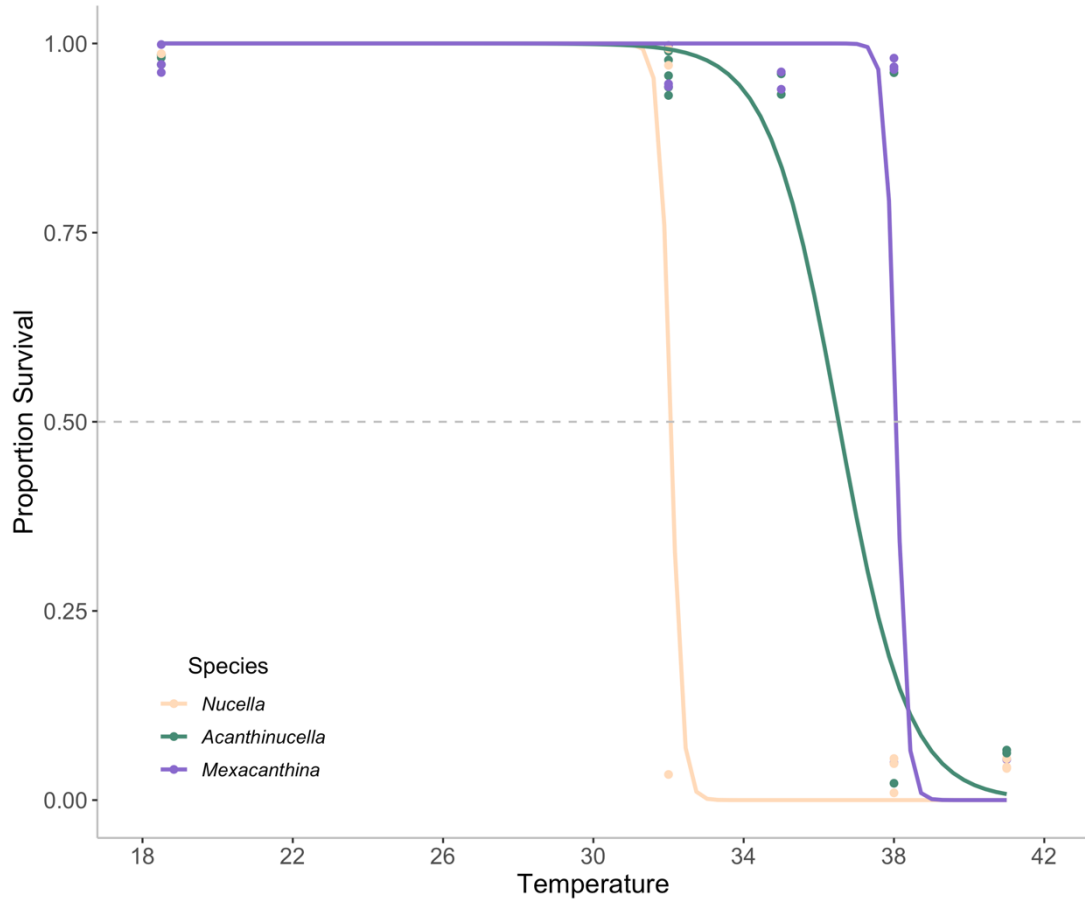


Figure 6. *Mexacanthina* and *Acanthinucella* are more heat tolerant than *Nucella*, with calculated LT_{50} values of 38.1°C, 36.5°C, and 32.1°C, respectively. Values shown are proportional survival following a 6-hr emersed thermal exposure and an 18-hr immersed recovery period at ambient seawater temperature, to which we have fit a logistic relationship. Points represent survival at each temperature treatment and are jittered for visibility.

Appendix

Table S1. Analysis of deviance tables for Gamma hurdle models (Wald Chi-Squared tests). We used a two-step model analyzing the effects of tidal elevation and *Mexacanthina* presence/density on native whelk presence (zero and non-zero data based on a binomial distribution model) and densities (non-zero data based on a gamma distribution).

Gamma Hurdle Model - *Mexacanthina* Presence

Binomial Distribution			Correlation of Fixed Effects		Random Effect
Parameter	χ^2	P	Elevation	<i>Mexacanthina</i>	Variance
Elevation	9.51	< 0.001	--	--	
<i>Mexacanthina</i>	16.61	0.002	0.287	--	0.26
Interaction	10.20	0.001	-0.417	-0.870	
Gamma Distribution					
Elevation	0.01	0.24	--	--	
<i>Mexacanthina</i>	1.40	0.91	0.528	--	0.08
Interaction	10.47	0.001	-0.670	-0.825	

Gamma Hurdle Model - *Mexacanthina* Density

Binomial Distribution			Correlation of Fixed Effects		Random Effect
Parameter	χ^2	P	Elevation	<i>Mexacanthina</i>	Variance
Elevation	14.97	< 0.001	--	--	
<i>Mexacanthina</i>	10.54	0.001	0.209	--	0.18
Interaction	8.58	0.003	-0.244	-0.977	
Gamma Distribution					
Elevation	1.19	0.21	--	--	
<i>Mexacanthina</i>	1.58	0.28	0.275	--	0.08
Interaction	4.72	0.03	-0.358	-0.941	

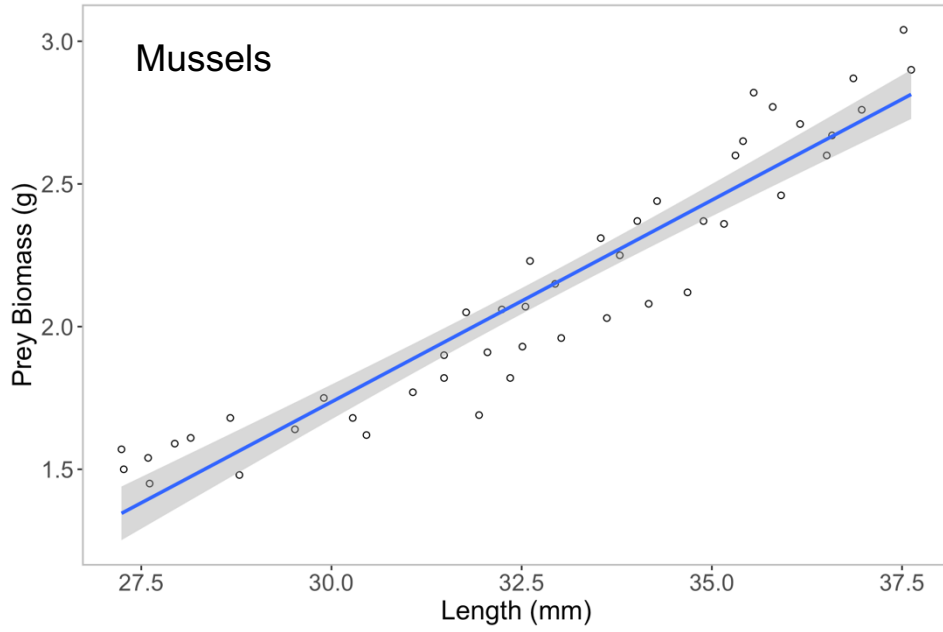
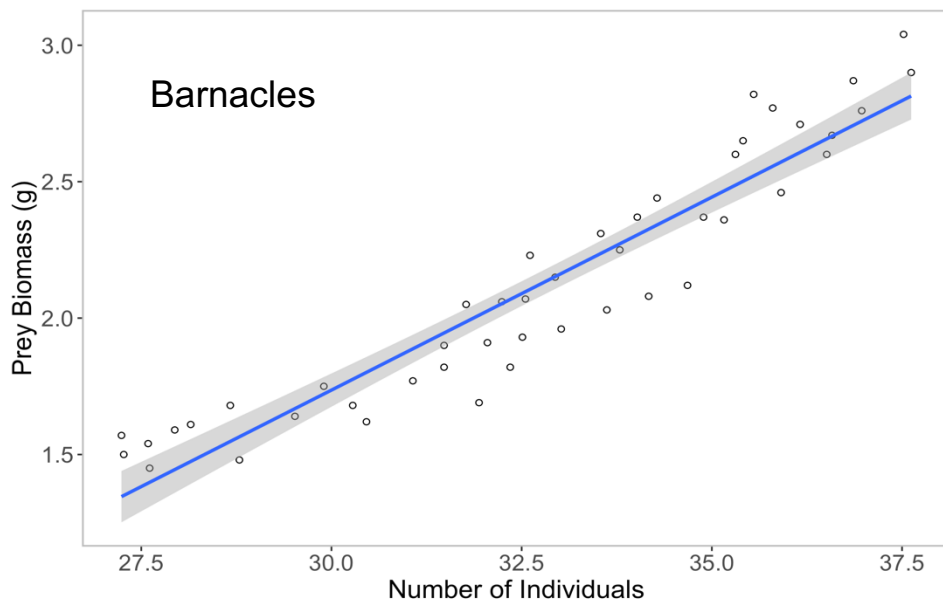
A**B**

Figure S1. Biomass regressions for (a) mussels, based on length x width ($R^2 = 0.89$), and (b) barnacles, based on counts of individuals ($R^2 = 0.83$).